Systematic Zoology

SOCIETY OF SYSTEMATIC ZOOLOGY

Museum
QL
1
S997

Museum Library

THE UNIVERSITY OF MICHIGAN
AUG 23 1960
MUSEUMS LIBRARY

Symposium: Invertebrate Classification and Phylogeny

Comments on the Phylogeny and Systematics of the Protozoa — *John O. Corliss* — 169

On the Origin and Phylogeny of the Coelenterates — *Cadet Hand* — 191

The Functions and Limitations of Classification — *R. E. Blackwelder* — 202

Ancestors, Embryos, and Symmetry — *M. J. Greenberg* — 212

VOLUME 8 DECEMBER 1959 NUMBER 4

Systematic Zoology

LIBBIE H. HYMAN, *Editor*

Editorial Board

C. L. HUBBS	1959	L. H. HYMAN
I. M. NEWELL	1960	S. W. MULLER
B. PATTERSON	1961	H. H. ROSS
C. D. MICHENER	1962	G. L. VOSS

SYSTEMATIC ZOOLOGY is published quarterly, on or about the tenth day of March, June, September, and December, by the Society of Systematic Zoology. Manuscripts and correspondence about the contents of the journal and other editorial matters should be addressed to the editor, Dr. Libbie H. Hyman, American Museum of Natural History, New York 24, New York.

Subscription rates are $4.00 to members, $7.00 to non-members and institutions. The price of single numbers, when available, is $1.50 to members and $2.00 to non-members. Annual dues are $2.00. Correspondence regarding subscriptions, purchases, non-receipt, and other non-editorial business should be addressed to the Business Manager, Dr. J. M. Savage, Dept. of Biology, Univ. of Southern California, Los Angeles 7, California. Correspondence concerning membership and other aspects of the Society's affairs should be addressed to the secretary-treasurer, Dr. R. E. Blackwelder, Dept. of Zoology, Southern Illinois Univ., Carbondale, Ill.

The Society of Systematic Zoology

OFFICERS FOR 1959

President.....LIBBIE H. HYMAN
American Museum of Natural History

President-Elect.....W. I. FOLLETT
California Academy of Sciences

Secretary-Treasurer.....R. E. BLACKWELDER
Southern Illinois University

THE COUNCIL

M. G. NETTING	1959	W. L. SCHMITT
W. H. BURT	1960	C. G. GOODCHILD
R. H. BAKER	1961	R. L. USINGER
J. W. WELLS	1962	H. VAN DER SCHALIE

Entered as second-class matter at the post office at Victor, New York, with an additional entry at Baltimore, Maryland

THE SOCIETY OF SYSTEMATIC ZOOLOGY

Systematic Zoology

VOLUME 8, 1959

NUMBERS 1–4

ISSUED 1959, BALTIMORE, MD., U. S. A.

Systematic Zoology

PUBLISHED BY

THE SOCIETY OF SYSTEMATIC ZOOLOGY

Editor

LIBBIE H. HYMAN
American Museum of Natural History
New York City

Editorial Board

C. L. HUBBS Scripps Institute of Oceanography	1959	L. H. HYMAN American Museum of Natural History
I. M. NEWELL University of California, Riverside	1960	S. W. MULLER Stanford University
B. PATTERSON Harvard University	1961	H. H. ROSS Illinois Natural History Survey
C. D. MICHENER University of Kansas	1962	G. L. VOSS University of Miami Marine Laboratory

The Society of Systematic Zoology

OFFICERS FOR 1959

President

LIBBIE H. HYMAN
American Museum of Natural History

President-Elect

W. I. FOLLETT
California Academy of Sciences

Secretary-Treasurer

R. E. BLACKWELDER
Southern Illinois University

THE COUNCIL

M. G. NETTING Carnegie Museum	1959	W. L. SCHMITT United States National Museum
W. H. BURT University of Michigan	1960	C. G. GOODCHILD Emory University
R. H. BAKER University of Kansas	1961	R. L. USINGER University of California
J. W. WELLS Cornell University	1962	H. VAN DER SCHALIE University of Michigan

Symposium: Invertebrate Classification and Phylogeny

THIS symposium, organized by Libbie Hyman of the American Museum of Natural History, was presented at the annual meeting of the Society of Systematic Zoology in Chicago, December 29, 1959.

Comments on the Systematics and Phylogeny of the Protozoa

JOHN O. CORLISS

Scientists run in a circle
and suppose
The secret sits in the middle
and knows (Robert Frost)

THE OUTLOOK for a good, defensible understanding of any phylogenetic relationships involving Protozoa is as discouraging as it ever was. Even "healthy speculation" must be based on such a paucity of decisive facts that it may be destined to be considered "healthy" by its author alone, and probably only for a short time even by him.

What are some of the reasons for such pessimism? The Protozoa (and even this term and the extent of the group it embraces are subjects of debate) present a number of rather formidable obstacles to the biologist interested in attempting to trace evolutionary relationships among the major groups. Let us consider these briefly.

Shortcomings of the Protozoa

(1) Their widespread lack of fossils. Exceptional groups, such as the Foraminiferida and Radiolarida, have left beautiful remains, but even these have proved to be of extremely limited value in tracing inter-group kinships. Thus the dimension of *time*, all-important in evolutionary considerations, can be brought in only indirectly, principally by assumption that selected representatives of present-day groups closely resemble ancestral forms which supposedly arose at different eras in the past history of the phylum.

(2) Their typically microscopic size. Again, there are a few exceptions; but these are practically of no aid in evolutionary considerations. Forced to await improved microscopical techniques, the protozoologist is still behind the systematists of other groups, even in the descriptive phase of his science. And (yet) over five hundred species have been described as new *annually*, on the average, during the past thirty years!

(3) Their subcellular organization. The protozoa, whether considered unicellular or acellular, are limited to structural diversities which, essentially, involve only the cytoplasm or the pellicle. Cytoplasmic organelles or pellicular characteristics, no matter how elaborate they may seem, hardly lend themselves to such convenient comparative study as the multicellular organ systems, skeletal elements, etc., of the Metazoa.

(4) Their ubiquity. Not only are Protozoa practically everywhere, but even

identical representatives of many minor taxonomic groups occur in widely distributed locations, geographically and ecologically speaking. Centers of dispersion, geographical ranges, restricted ecological niches, etc., involve concepts seldom applicable to protozoan species, thus compounding the difficulties of tracing relationships and evolutionary histories.

(5) The frequent absence of sexuality. If not absent, at least sexuality is yet to be discovered among many groups of present-day protozoa. Not only are experimental genetic approaches to phylogenetic problems rendered virtually impossible at the species level, but the very mechanisms responsible for origin and evolution of entire groups among other organisms seemingly have been, or are now being, by-passed by a number of Protozoa.

(6) The very fact that a protozoan cannot even be defined to everyone's general satisfaction. Their nature is complex, their ancestry obscure, their diversity in form, structure, size, and habitat great. A definition reading, "Present-day protozoa are *simple, minute, unicellular, primitive, animal* organisms" is susceptible to attack on all five counts.

Bases for Classification Schemes

Since schemes of classification ideally should reflect phylogenetic relationships among the several groups of organisms involved, the taxonomically-minded protozoologist is forced to utilize all evidence which appears to be reasonably substantial even if only inferential.

Morphological considerations continue to form the basis of systematics in protozoology, at both lower and higher taxonomic levels. As yet, the basis cannot be otherwise. Still, recent advances of importance have been made along these main lines:

(1) Greater utilization of supplementary *non-morphological* data. Physiological or biochemical, genetic, ecological, and morphogenetic factors are becoming of increasing importance as our knowledge grows in these principally experimental areas of research.

(2) Renewed emphasis on the *comparative* approach. Whether the characteristics are morphological, physiological, or otherwise in nature, their analysis over a whole population or range of forms can be rewarding from the taxonomic point of view. Application of statistical methods in treatment of the comparative data obtained is often advisable.

(3) Attention to the *entire* life cycle. Whether the organisms involved are free-living or symbiotic (including parasitic), knowledge of all stages in polymorphic life histories is of paramount value in determining relationships. If phylogeny is defined as "a continuum of ontogenies in the course of evolution," then no ontogeny should be neglected.

(4) Application of *new or improved techniques* of study. Obviously the development of precise cytochemical-biophysical tests, of phase and electron microscopy, and of other modern technical approaches applicable in protozoology has made possible the gathering of new and more refined data directly utilizable in systematics. In the past quarter of a century the advent and refinement of silver impregnation methods and of the Feulgen nucleal reaction have, alone, been nearly indispensable to investigators engaged in significant revisions at the higher taxonomic levels.

Several arbitrarily selected examples of controversial problems in the systematics of the Protozoa will serve to illustrate the points made in the preceding sections of this paper. The examples are purposely concerned with the higher ranks only.

The Phylum PROTOZOA

A number of modern biologists consider that the best which can be said for the term "Protozoa" is that it is firmly entrenched in the literature. Recognition of the "Protozoa" as comprising a single, homogeneous phylum of animal organisms also is sometimes held to be more of

a practical convenience, dictated by custom, than a reflection of the probable relationship in nature of the diverse organisms involved. Two recent alternatives, from among the several which exist in the literature to date, may be mentioned (also see Whittaker, 1959). Dougherty (1955) revives the term Protista for an assemblage of organisms embracing all the usual "Protozoa" plus the higher algae and all the fungi. Copeland (1956) distributes the "Protozoa" among some five phyla which, with three others, comprise his kingdom Protoctista.

One must agree that informed attempts to revise tradition-bound systems of the lower organisms are to be encouraged. The essays are never premature, but their wide acceptance may be, especially if adoption is uncritically made. In view of the diversity among the solutions proposed and the paucity of pertinent data available, I believe that carrying on for a while longer with the standard "phylum PROTOZOA" is virtually demanded on the basis of practical necessity. Such an arbitrary decision is subject to subsequent modification when accumulated facts better support an alternative arrangement.

The problems of group relationships *within* the over-all protozoan assemblage seem somewhat more tangible, although their solutions are similarly fraught with many difficulties. It is, however, becoming increasingly disturbing to modern protozoologists to retain as groups of equal rank the four conventional subdivisions established as classes long ago by Bütschli (1880-1889): the Sarcodina (originally "Sarkodina"), Sporozoa, Mastigophora, and Infusoria (=Ciliophora). A concise history of protozoan classification since the times of O. F. Müller in the 18th century has been traced by Hall (1953). The following discussions are limited to major problems involving Bütschli's four classes, now widely accorded the status of subphyla (e.g., see Calkins, 1933; Jahn and Jahn, 1949; Grassé, 1952; Hall, 1953; Hyman, 1959).

The Sarcodina-Mastigophora Complex

Kudo (1954, p. 417) has echoed the general sentiment of many protozoologists in his comment that "it is sometimes very difficult to distinguish the Sarcodina and the Mastigophora." Hyman (1959, p. 711) discusses the matter in greater detail, stating very plainly, "The author. . . . cannot find it justifiable to separate flagellates and rhizopods by a gap as great as subphylum. . .[in fact] the author wonders whether. . .[they] should even be separated by a rank as great as class."

There are weaknesses in each of several possible solutions. To those systematists who may feel that both groups already are polyphyletic in origin, combining them into a single subphylum is distasteful. Reducing their independence to a still greater extent, by combining them with the group known as the Sporozoa under Doflein's subphylum Plasmodroma, is even more drastic. Furthermore, such a combination is held together solely on the basis of a single, negative characteristic; viz., they are all *non*-ciliate Protozoa (Doflein's second subphylum being the Ciliophora). Through the great influence of Doflein and Reichenow (now in its 6th edition, 1949-1953), the latter course of action has been favored for many years (e.g., see Kudo, now in its 4th edition, 1954). However, the "classes" Sarcodina, Mastigophora, and Sporozoa actually are being accorded equal rank with the "classes" Ciliata and Suctoria.

Grassé (1952), who treats the Protozoa as a branch of a "phylum" Protista, unites the rhizopod sarcodinids with the phyto- and zooflagellates in a single "sub-branch" Rhizoflagellata. This arrangement may meet with wide acceptance. Copeland's (1956) phylum Protoplasta is more inclusive, embracing the Actinopoda of the literature in addition to the Rhizopoda and Mastigophora; this may represent a slight improvement over Grassé's scheme.

The closeness of flagellates and rhizopods cannot be denied. Striking evidence is seen in the many examples among

present-day forms of amoeba-flagellate reversibility in the life cycle of single species[1] (see Pl. I, Figs. 3–5). One need not mention other facts, such as the existence of species equipped simultaneously with both flagella and pseudopodia (Pl. I, Figs. 1, 2), and the occurrence of flagellated gametes among sarcodinids and pseudopodia in some flagellates. The remarkable case of the trichomonad *Gigantomonas herculea,* member of an order of "higher" zooflagellates, deserves special mention. Kirby's (1946) painstaking investigation of its whole life cycle revealed that an amoeboid stage is extremely reminiscent of the commonly binucleate stage of the sarcodinid(?) species *Dientamoeba fragilis* (see Pl. I, Fig. 5A, B). In its mode of nuclear division *Gigantomonas* resembles both *Dientamoeba* and *Histomonas,* a "lower" *zooflagellate.* The possible phylogenetic significance of the morphological similarities between the latter two genera had been mentioned before Kirby, by Dobell (1940) and Wenrich (1944).

Based primarily on a detailed survey of the pertinent literature, discussion of all of which is naturally beyond the scope of these comments, I should like to offer the following suggestions in a tentative solution of the "Sarcodina-Mastigophora problem": (1) Let subphylum I of the phylum PROTOZOA embrace all the controversial amoeboflagellate groups under discussion; I propose the name MASTIGAMOEBAEA for this subphylum. (2) Recognize three major subdivisions, superclasses, of the Mastigamoebaea: the Rhizoflagellata, the Actinopoda, the Paraflagellata. (3) List as classes of the superclass Rhizoflagellata the Flagellata and the Rhizopoda, retaining for taxonomic convenience the Phytomastigophora and Zoomastigophora as subclasses of the Flagellata and recognizing possibly three subclasses (or orders?) within the Rhizopoda.[2] (4) Include in the superclass Actinopoda, as classes or perhaps only as orders, these groups: the Heliozoida, the Acantharida, the Radiolarida. (5) Consider the superclass Paraflagellata to be represented by a single order of aberrant, highly evolved flagellates, the Opalinida (see Corliss, 1955, and below).

There is little originality in this five-point proposal, nor do I so claim. But I believe it offers a compromising solution of some value, by combining what I consider the better features of a variety of conflicting views in the literature. Ranks are not unduly raised, unfamiliar names are not created or exhumed wholesale, unrecognizable combinations of well-known groups are not suggested. While fairly conservative, the proposal nonetheless attempts to incorporate recent ideas when they seem sounder, as several of them do, than traditional beliefs.

The Pigmented Flagellates

There is no need to be troubled by the fact that many botanists lay taxonomic claim to the "algal flagellates."[3] Recognition of the common ancestry of green plants and various protozoan groups does not oblige the systematic protozoologist

[1] A striking laboratory demonstration of the rapid transfer of an organism from the "class Mastigophora" to the "class Sarcodina" may be seen in the most interesting experimental work on *Tetramitus rostratus* by Brent (1957), using nitrogen mustard as the inducing agent.

[2] Precise recognition of different types of protoplasmic streaming in various kinds of pseudopodia has been and should continue to be of real help, as new data accrue, in sorting out sub-groups within the Rhizopoda. Some of the taxonomic implications of refined investigation of pseudopodial flow are mentioned in a very recent work by Jahn and Rinaldi (1959); a stimulating and pertinent review of theories of amoeboid movement in general has been offered by Noland (1957).

[3] Incidentally, modern biochemical studies on the pigments of these forms, being carried out with fervor by both "botanists" and "zoologists," are becoming increasingly important in the phylogenetic implications of the data obtained. For example, see the very recent outburst of reports on cryptomonad pigments in a single number of Nature (Allen et al., 1959; Haxo and Fork, 1959; ÓhEocha and Raftery, 1959).

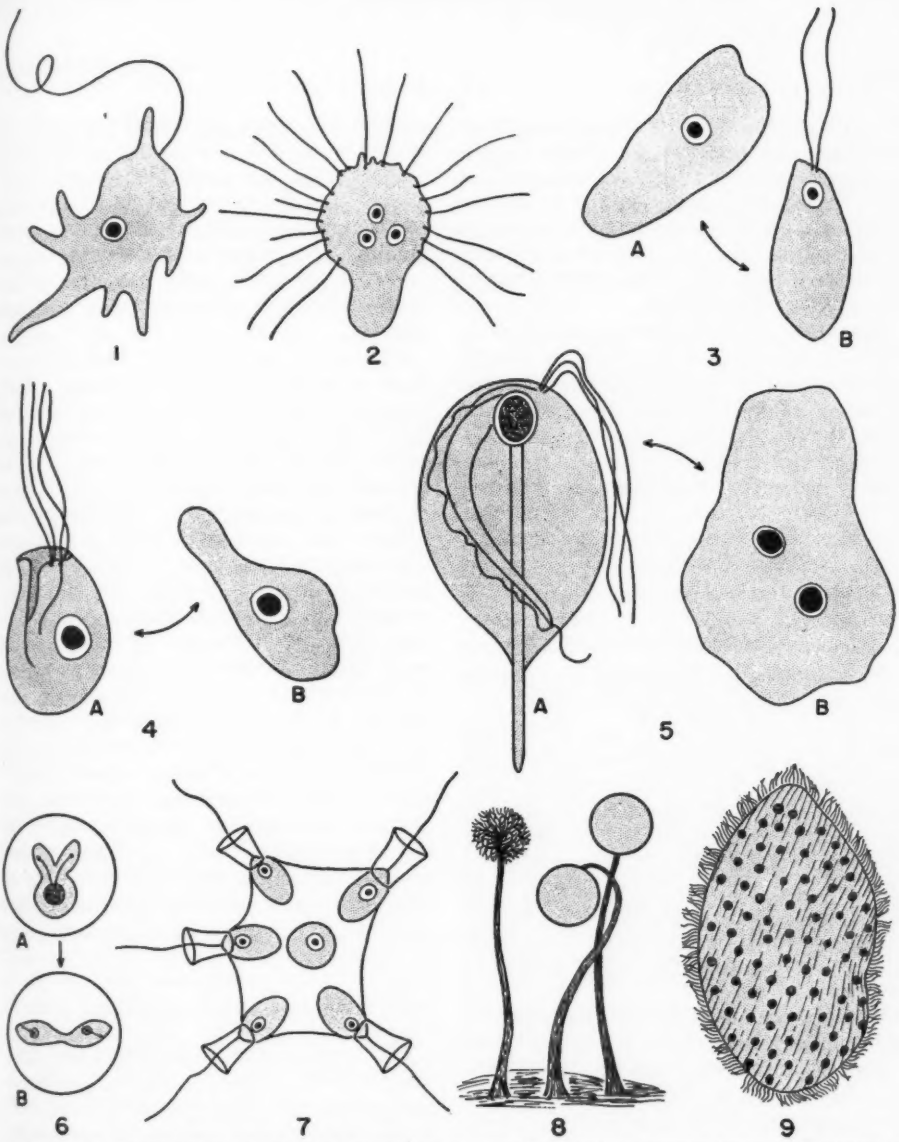

PLATE I. Illustration of selected examples of organisms whose proper taxonomic status is problematical. The figures are somewhat schematically redrawn, with deliberate omission of certain cytoplasmic inclusions and contractile vacuoles, from various sources in the literature. FIG. 1. *Mastigamoeba* sp., a rhizopod-flagellate possessing several pseudopodia and a single long flagellum. FIG. 2. *Multicilia* sp., a curious multiflagellated form capable of amoeboid locomotion as well. FIG. 3. *Naegleria gruberi* (also known under other generic names), a dimorphic species in which the amoeboid phase (A) dominates the flagellate phase (B). FIG. 4. *Tetramitus rostratus,* a dimorphic species in which the quadriflagellated form (A) is predominant; but a completely amoeboid form (B) also occurs in the full life cycle. FIG. 5. *Gigantomonas herculea,* a complex trichomonad flagellate (A) with amoeboid stage (B) strikingly reminiscent of *Dientamoeba fragilis.* FIG. 6. *Babesia bigemina,* an enigmatic blood parasite of cattle, shown within an erythrocyte. Early (A) and a later (B) stage of fission reveal the curious flagellate nature of its division process. FIG. 7. *Proterospongia haeckelii,* a choanoflagellate considered to be on the ancestral line leading to the sponges. FIG. 8. *Comatricha* sp., a "eumycetozoan" representing a whole group whose taxonomic affinities are controversial. FIG. 9. *Opalina* sp.: a flagellate or a ciliate?

to remove the phytomastigophorans from his taxonomic schemes, as Calkins (1933), in a move followed by few, attempted to do. Copeland (1956), acting somewhat similarly, places the colored flagellates in his phylum Pyrrhophyta, considerably separated from the Zoomastigophora in the phylum Protoplasta.

To separate by a distinct kingdom or phylum, or even subphylum, forms as closely related as certain colored and colorless flagellates is hardly justifiable from the point of view of probable phylogenetic relationships. The ease of experimental induction of apochlorosis in laboratory-grown cultures of chromatophore-bearing flagellates (e.g., see Pringsheim, 1948; DeDeken-Grenson, 1959) supports this conclusion rather dramatically.

The Enigmatic Mycetozoa

Hyman (1940) has summarily excluded this rather extensive group from the protozoological realm with the statement, "Since the plasmodium eventually puts forth sporangia filled with spores, we here regard the myxomycetes as fungi and omit them from consideration." This is a convenient decision which I am tempted to endorse without further comment. Unfortunately, there are complications the details of which cannot be discussed here. But let us consider the major problems briefly.

The Myxomycetes of the botanists are not identical with de Bary's entire order Mycetozoa, as protozoologists commonly suppose. In addition to these forms, sometimes known as the Myxomycetales, which the mycologists generally recognize as a class of true fungi (e.g., see Macbride and Martin, 1934), the Acrasiales, Plasmodiophorales, and Labyrinthulales are often allocated to the Mycetozoa, too. Bonner (1959) has summed this well, "They are placed together because they represent four anomalous groups of unknown origin . . . they probably have little or no relation one to another."

Hall (1953) and Kudo (1954) place the enigmatic genus *Labyrinthula* and its relatives in the sarcodinid order Proteomyxidiida; the other groups mentioned above, in the Mycetozoida. Copeland (1956) makes the separation a little more positive by allocating *Labyrinthula* to an order of his class Sarkodina, the others each to separate orders in his class Mycetozoa.

Formal dropping of at least some of these fungal or fungus-like groups of organisms from the phylum Protozoa appears advisable. The "Eumycetozoa" or Myxomycetes would clearly seem to be lower fungi [4] (see Pl. I, Fig. 8). The Plasmodiophorales may well belong in the fungal class Phycomycetes or perhaps in a new class of their own, as the mycologist Sparrow (1958) has very recently suggested. The Labyrinthulales appear to remain entirely enigmatic. Perhaps the Acrasiales should be appended, as a "group of uncertain status," to our class Rhizopoda: by its lack of a flagellated stage, sexuality, and a true plasmodium it is far different from the Myxomycetes or "true" slime molds. The common appearance of myxamoebae and/or myxoflagellates in the life cycle of all the "Mycetozoa" clearly indicates a protozoan ancestry in the distant past. But this need not oblige us to embrace the entire assemblage as Protozoa today.

The Opalinid Infusorians

The controversy over Metcalf's "protociliates" has flared up anew in very recent years, triggered by Grassé's (1952) placement of them among the zooflagellates. Many of the arguments, old and modern, were reviewed a fairly short time

[4] G. W. Martin's presentation in a mycological symposium, scheduled to follow by one day the program in which the present paper is being read, will surely contain remarks pertinent to the questions I have raised here. The symposium referred to is concerned with classification of fungal groups of debatable affinity, and Dr. Martin's talk is entitled, "The Systematic Position of the Myxomycetes."

ago (Corliss, 1955) and thus need not be repeated here.

Probably the most recent investigation bearing directly on the systematic status of these enigmatic Protozoa is that of Wessenberg (1957), a work unfortunately not yet available in a full publication. Wessenberg has traced the morphogenetic changes occurring during the whole life cycle of several opalinids and has found, among other noteworthy discoveries, that both "longitudinal" (interkinetal or symmetrogenic) and "transverse" (perkinetal or homothetogenic) fissions may take place. It is the alleged predominance of a symmetrogenic flagellate-type fission, plus the nuclear monomorphism and the occurrence of anisogamous gametes, which has influenced some protozoologists to classify the opalinids with the Flagellata. Details of Wessenberg's significant find of perkinetal division are thus awaited with interest.

From his examination of the nuclear apparatus in *Opalina ranarum* and *Cepedea dimidiata,* Devidé (1951) concluded that there is a "temporary existing of nuclear dimorphism in opalinids." This interpretation of the cytological picture in the forms studied is used by Devidé in support of the opalinids' affinity with "euciliates." To my knowledge, no one has ever commented critically on this work in the past nine years. Raikov (1958), interestingly enough, does not even mention the opalinids in his stimulating theory concerning the origin of nuclear dualism in ciliates.

Surely most protozoologists today will agree with the reasonable supposition that the opalinids probably have enjoyed a very long evolutionary history of their own, quite independent from other phyletic lines within the phylum. Appending them to either the zooflagellates or the ciliates may be a point of little significance. Because to me they clearly do not seem to be "protociliates" (a theoretical primitive ancestral group within the Ciliophora) or even the "missing link" between flagellates and ciliates, I favor assigning them to a separate superclass within the large subphylum Mastigamoebaea (see above). In such a recommendation I am considering them less closely associated with "true" zooflagellates than I have previously (Corliss, 1955). Eventually more such careful investigations as those already carried out by Chen (1948), Devidé (1951), Mohr (1959), Noirot-Timothée (1958), Pitelka (1956), Wessenberg (1957), and Yang (1960), although primarily non-systematic in nature, will result in new data of significant value to the taxonomist. It is profitless to discuss the problem further at the present time.

My comments on the opalinid problem might appropriately be terminated with two quotations from the works of Hyman (1940, 1959). In 1940, classifying the group as ciliates, she nevertheless pointed out that "opalinids differ from the typical ciliates in almost every respect except the possession of cilia" (see Pl. I, Fig. 9). Even this "difference" is, of course, weakened by the revelation of the basic anatomical identity of cilia and flagella, through use of electron microscopy (see such recent works and reviews as those by Bradfield, 1955; Ehret and Powers, 1959; Fauré-Fremiet, 1957a, 1958a; Pitelka, 1959; Pitelka and Schooley, 1955; Roth, 1957, 1959). But in 1959, Hyman has offered a conclusion with which no protozoologist should quarrel, ". . . further research on the group is [still] necessary to establish its systematic position."

The Polyphyletic Sporozoa

No one is in greater agreement with the suggestion that the Sporozoa represent a heterogeneous taxonomic group of polyphyletic origin than the experts on the group themselves (e.g., see Ball, 1960). The problem is made difficult for the general protozoologist not so much because proposed resolutions are in disagreement with one another but because they are practically non-existent. The class or subphylum "Sporozoa" has enjoyed a long

life as a fairly respectable, seemingly integrated group of Protozoa, principally bound together, however, by three purely negative characteristics [5]: its species are generally minute; they are all internal parasites of other organisms; their vegetative stages possess none of the organelles of locomotion typical of other Protozoa. That the difficulties of deducing their affinities with other protozoan taxa, or even determining interrelationships among their own groups, are magnified by these very properties must be appreciated.

Over fifty years ago, Schaudinn, Hartmann, and others suggested two main divisions of "Sporozoa," to be considered of equal rank: the Telosporidia and the Neosporidia. Wenyon (1926) made the independence of these "sporozoan" groups abundantly clear by retaining the well-known name Sporozoa for the first class and using Doflein's ordinal name Cnidosporidia for the second class (Poche, 1913, had also used these names before Wenyon). Concerned over the nature of the basis used in distinguishing these two groups and over disrupting more popular usage, however, current authoritative textbooks in the United States (Hall, 1953; Kudo, 1954) have not supported the proposal of separate taxa at the subphylum level. On the other hand, the French have followed Wenyon's lead quite faithfully (Grassé, 1953).

The striking uniqueness of the cnidosporidian spore, equipped as it typically is with a distinctive membrane (composed of one or more valves), one to four polar filaments (commonly encased in polar capsules until extruded), and one to many amoeboid sporoplasms, justifies the separate high-level systematic position accorded the species possessing it. Characteristics of the Sporozoa *sensu stricto* include production of sporozoites, a much simpler "spore" stage (if present at all), more complicated life cycles, and wider distribution in a greater variety of hosts. Thus recognition of both a subphylum SPOROZOA and a subphylum CNIDOSPORIDIA seems highly advisable. The former would contain two classes, the Gregarinomorpha and the Coccidiomorpha, each with two orders. The latter would contain no classes, dropping directly to some four or five ordinal groups. The curious Haplosporidia, treated as "acnidosporidians" in current textbooks, should perhaps be appended to the Sporozoa as a group of uncertain taxonomic status.

[5] I am deliberately omitting mention of their allegedly universal possession of a "spore": partly because it is not an entirely unique characteristic and partly because of the regrettable lack of homology among the stages designated as the "spore" in the several groups conventionally assigned to the subphylum "Sporozoa."

Sarcosporidians: True Protozoa?

A "sporozoan" group whose systematic affinities are as enigmatic as those of the "Mycetozoa" (treated above), although its members have been studied far less extensively, is the Sarcosporidia. Conventionally this small group is included in taxonomic schemes as an order or subclass of the Sporozoa *sensu lato*. On the basis of the fungal affinities reported by Spindler (1947) and Spindler and Zimmerman (1945), Hyman (1959) is quite willing to eliminate it from the phylum. Grassé (1953), however, does not consider Spindler's investigations, to date reported only in brief, to be so convincing.

Fuller accounts are needed concerning these curious muscle parasites. Even if some of them should appear to be "true" Protozoa, it is likely that their affinities with either the Sporozoa or the Cnidosporidia will remain enigmatic. A happy solution to the perplexing situation concerning the taxonomy of these forms, from the point of view of the protozoologist, would be to transfer the problem intact to the mycologist, as Hyman (1959) already has proposed.

The Position of Babesia

Among the innumerable scattered problems at the lower taxonomic levels within the subphyla Sporozoa and Cnidosporidia,

one may be mentioned here which is perhaps potentially of greater phylogenetic significance than many.

Species of the economically important genus *Babesia* (Pl. I, Fig. 6A, B) pass one stage of their life cycle in the tissues of ticks, the vector host; a second stage is spent in the erythrocytes of cattle. The polymorphism exhibited by these Protozoa and their near relatives has caused their allocation to widely separated taxonomic groups at various times by different workers. They have been considered to be haemosporidians, haemoflagellates, and even rhizopods. A conventional location is that adopted by Kudo (1954) who places them in a family neighboring the malarial Plasmodiidae and the related Haemoproteidae, all in the sporozoan order Haemosporidiida. Hall (1953) separates *Babesia* from the two haemosporidian families just mentioned by assigning it to an order of its own. In Grassé (1953), *Babesia* and its alleged close relatives are considered as "uncertain Sporozoa."

In one of the most recent systematic considerations of this and other enigmatic "sporozoan" genera, Biocca (1957, 1958) places *Babesia* in an order within a new class "Toxoplasmatea," quite separate from his other homokaryote classes (including the "Sporozoea" and the "Cnidosporidiea"). This worker, incidentally, follows Jírovec et al. (1953), Piekarski (1954), Raabe (1948), Ulrich (1950), and others, in separating the opalinids from the ciliates on the basis of the heterocaryote nature of the latter. Sarcosporidians (discussed above) are allocated by Biocca to another order within his "Toxoplasmatea."

The essentially symmetrogenic type of fission which occurs in the erythrocytic stage of *Babesia's* life cycle (Pl. I, Fig. 6A,B), along with the other flagellate features revealed in the careful studies by Dennis (1930, 1932), suggests a phylogenetic affinity with the flagellates which warrants further investigation. The life-history similarities between the well-established sporozoan genus *Plasmodium* and the enigmatic genus *Babesia* are mostly superficial. Thus maintenance of a close taxonomic relationship between these two genera seems highly inadvisable.

Problems Within the Ciliophora

In a number of respects the assemblage of ciliated Protozoa may be looked upon with envy by systematists devoting their efforts to study of the other major groups. Although the exact origin of ciliates probably is destined to remain enshrouded in mystery, there always has been general agreement among protozoologists on three main points: the strong likelihood of their flagellate ancestry; the compactness of the group within itself; and the supposition that the Ciliophora represent the peak of evolutionary development within the phylum Protozoa. Incidentally, the most likely candidates among present-day forms for the label of "most primitive ciliates" would appear to be the rhabdophorine gymnostomes. A number of protozoologists still endorse an older view that the parasitic astomes were first, a conclusion apparently based on the fact that these forms are mouthless. But the astomatous condition doubtless represents a secondary acquisition correlated with the mode of life of these ciliates.

A number of problems related to various levels of ciliate systematics—phylogeny and evolution, schemes of classification, and nomenclature—have been treated in some detail in a recent series of papers by the writer (Corliss, 1956, 1957a, 1958, 1959a,b, 1960). The resurgence of interest in the taxonomy of major ciliate groups has been brought about principally by the publication of a heuristic paper by Fauré-Fremiet (1950). Fauré-Fremiet proposed a scheme of classification that represents the first extensive revision of the Ciliophora since Stein's (1867) establishment of the system which, in a form augmented and refined by Kahl (1930–1935), is still in wide usage. This new classification, to some extent modified and expanded (see Corliss, 1956, and especially 1958), is presented in

the form of an illustrated "phylogenetic tree" in Plate II.

Three problems, chosen from areas of greatest controversy, are discussed briefly below. Others must be considered beyond the scope of the present paper, although one—the question of the position of the enigmatic opalinids (Metcalf's "Protociliata" group)—has been considered above. The knotty problem of the exact affinities of the astomes (e.g., should they be totally absorbed by other existing ordinal groups?) is a fascinating one (see de Puytorac, 1954, 1959; Corliss, 1956, 1959a), as is also the matter of the gymnostome-hymenostome interrelationships (Corliss, 1958). The subclass Spirotricha, incidentally, appears to be in little need of revision: its six included orders are characterized by possession of more highly developed compound ciliature than that found among the Holotricha. It might be pointed out that the smallest of the spirotrich orders needs to be known by the less familiar name of Odontostomatida, since its former name, "Ctenostomatida," is preoccupied (Corliss, 1957a).

Chonotrich-Gymnostome Affinities

The chonotrichs have represented a vexatious problem to systematic protozoologists for many decades. Tracing the past taxonomic history of the seemingly enigmatic group is beyond the scope of the present abbreviated treatment of the problem. But modern comparative studies concerned with the morphogenetics of their ontogeny (Guilcher, 1951), their unusual macronuclear structure (Fauré-Fremiet, 1957b; Tuffrau, 1953), and the ultrastructural nature and mode of production of their non-contractile stalk (Fauré-Fremiet *et al.*, 1956) have erased the enigma of their kinship with other ciliates. In these investigations, as well as others not cited, careful comparison with the similar characteristics or phenomena exhibited by the cyrtophorine gymnostomes reveals that affinities between the two groups must be very close.

Thus the order Chonotrichida can now be placed among the lower holotrichs with considerable assurance that such a taxonomic decision does not contradict the phylogenetic history of the group, as that history is reconstructed from intensive comparative study of present-day forms.

The Peritrich Controversy

Acceptance of the peritrich ciliates as "good" members of the first great subclass of the Ciliophora, the Holotricha, seems to be meeting with more resistance than the similar subordination of the chonotrichs (e.g., see Hyman, 1959; Finley et al., 1959). Detailed reconsideration of this difficult problem is out of place here (see Corliss, 1956). Recognition of the order Peritrichida as last in a phylogenetic sequence commencing with the pleuronematine Hymenostomatida is, admittedly, based on a number of interpretations of data available only for present-day representatives of the several groups involved. Furthermore, certain mysteries continue to defy even speculation, such as the polarity of the peritrich body.

I think that there is a fair reply, however, to the type of criticism offered by Finley et al. (1959) who more or less intimated that the peritrichs, by their possession of unique characteristics, should be separated from all other ciliates and, indeed, should be considered as the most highly evolved of all groups. Most, if not all, "unique" features revealed in species of peritrichs are also found in a number of members of one or more other "good" orders of holotrichs: stalk, scopula, sedentary life, migratory larval stage, modes of fission and conjugation, and, although not as obviously, even the oral ciliature (especially when its infraciliature is studied from a comparative point of view). Furthermore—and this is an important point perhaps often overlooked by specialists of isolated groups—*every* order of present-day ciliates very likely has enjoyed a long evolutionary history of its own and thus can boast of remarkably

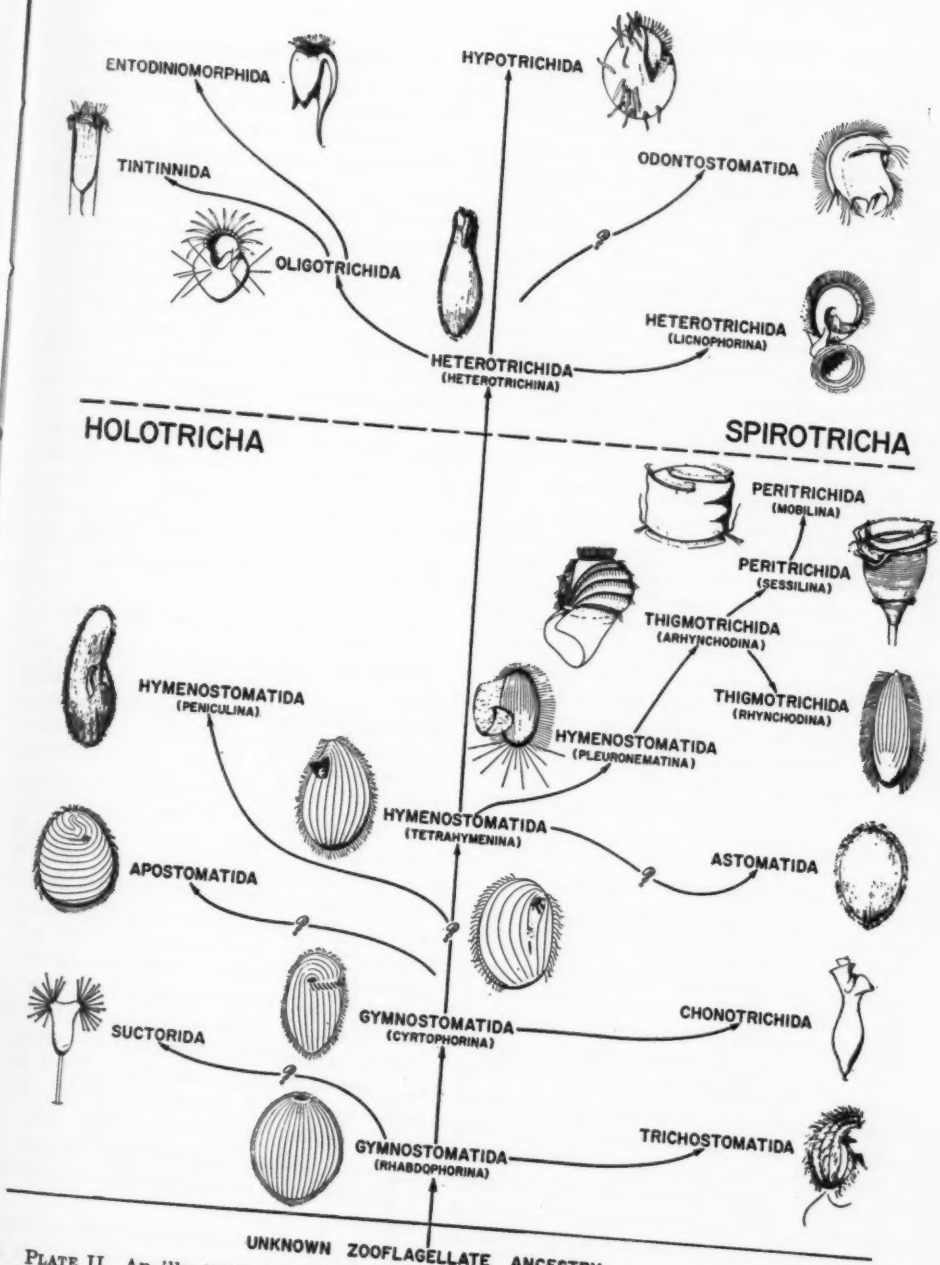

PLATE II. An illustrated genealogical tree of the ciliated Protozoa. Although necessarily oversimplified, the drawing represents an attempt to show main evolutionary lines in the proposed phylogeny of orders and suborders comprising the subphylum Ciliophora. See text for discussion of some of the principal problems involved. The inset figures have been redrawn from various sources in the literature.

"unique" structures. I submit that many of these rival any unusual feature of the peritrichs. To mention a few very briefly: the curious tentaculoids and remarkable loricae of tintinnids; the absolutely unique rosette and amazing life cycles of apostomes; the elaborate holdfast organelles of certain astomes; the well-developed gland-like organelle of chonotrichs and some gymnostomes; the thoroughly enigmatic "statocysts" of certain gymnostomes; the unrivalled tentacles of several gymnostome genera; the puzzling watchglass organelle of all ophryoglenid hymenostomes; the incredible toxic trichocysts of gymnostomes; the fantastically developed compound ciliary organelles of certain hypotrichs; the conspicuous skeletal plates and other unique anatomical features of entodiniomorphids; the catenoid colonies of astomes; the remarkable loricae of certain trichostomes; the bizarre body forms, often correlated with unusual habitats, of innumerable species belonging to many orders of both holotrichs and spirotrichs; the diversified, polymorphic life cycles seen in many orders, particularly among suctorians, chonotrichs, apostomes, trichostomes, hymenostomes, and thigmotrichs.

The Suctorian Ciliates

Perhaps the most unusual, in more ways than one, of all ciliates are the suctorians, a group in which the development long ago of the sedentary habit probably has been responsible for most of its specializations only uncommonly seen in other groups. Classically the Suctorida have been treated as a taxonomic group more distinct from "true" ciliates than the chonotrichs, the peritrichs, or even the opalinids. Based principally on the comprehensive treatments and hypotheses of Kahl (1931) and, more recently, of Guilcher (1951) and Fauré-Fremiet (1950), however, there has been a strong trend towards closing up the gap between these forms and the holotrich ciliates (e.g., contrast Doflein and Reichenow, 1927–1929 and 1949–1953; and see comments in Hall, 1953, and in Hyman, 1940, 1959).

The "unique" structures seen in suctorians, somewhat paralleling the situation discussed above for those of the peritrichs, are, for the most part, possessed by certain members of other groups: budding is found among species of several holotrich orders; the scopula and stalk are found in peritrichs, and their homologues presumably in thigmotrichs and hymenostomes; tentacles, although probably of a different sort, are possessed by some gymnostomes and thigmotrichs; the sessile, attached stage, even its lack of external ciliature, is not restricted to suctorian ciliates but is found elsewhere, too (e.g., in certain thigmotrichs). Thus recognition of these curious Protozoa as comprising an order Suctorida within the subclass Holotricha seems justified.

Phylogenetic Trees for Protozoa

To my knowledge only two serious attempts to construct a fairly detailed genealogical tree embracing all protozoan groups have been published. These both appeared over 75 years ago (Bütschli, 1880; Kent, 1880): see Plates III and IV. The "shortcomings" of the Protozoa discussed early in this paper, particularly their lack of a fossil record of any value in comparative evolutionary studies involving the higher taxa, make it readily understandable why phylogenetic trees have been so scarce in the literature. In spite of these, and other practical objections such as the extreme difficulty of expressing complex interrelationships in a simplified, two-dimensional scheme, I have suggested a new tree myself (see Pl. V). Possible justification for such a bold action is my use of this speculative dendrogram to illustrate some of the points discussed in following paragraphs.

Before proceeding further, let us recall the important assumption on which all subsequent remarks in this section are based: that certain present-day forms have gone essentially unchanged for per-

haps hundreds of millions of years [6] and thus modern protozoologists can consider that they are dealing with forms closely resembling postulated primitive species. Under this assumption the factor of *time*, indispensable in any truly phylogenetic considerations, is not neglected. The expression *phylogenetic tree* is employed with the clear understanding that even the addition of quotation marks (*"phylogenetic" tree*) would hardly make it justifiable from the point of view of a purist. I have also used the basic evolutionary principle that there is a positive correspondence between degree of similarity of organisms and their recency of common ancestry. This principle has been severely criticized recently by Bigelow (1958), but Bader (1958) has, in my opinion, most competently invalidated Bigelow's objections; thus the matter requires no discussion here.

According to older views (e.g., see Pl. IV), the "simple" rhizopod "Sarcodina"

[6] There is a considerable mass of factual data in support of this; e.g., see the very recent note by Madison (1958) in which members of quite advanced phytomastigophoran orders are reported from sediments estimated to be from 2.6 to 2.8 billions of years old.

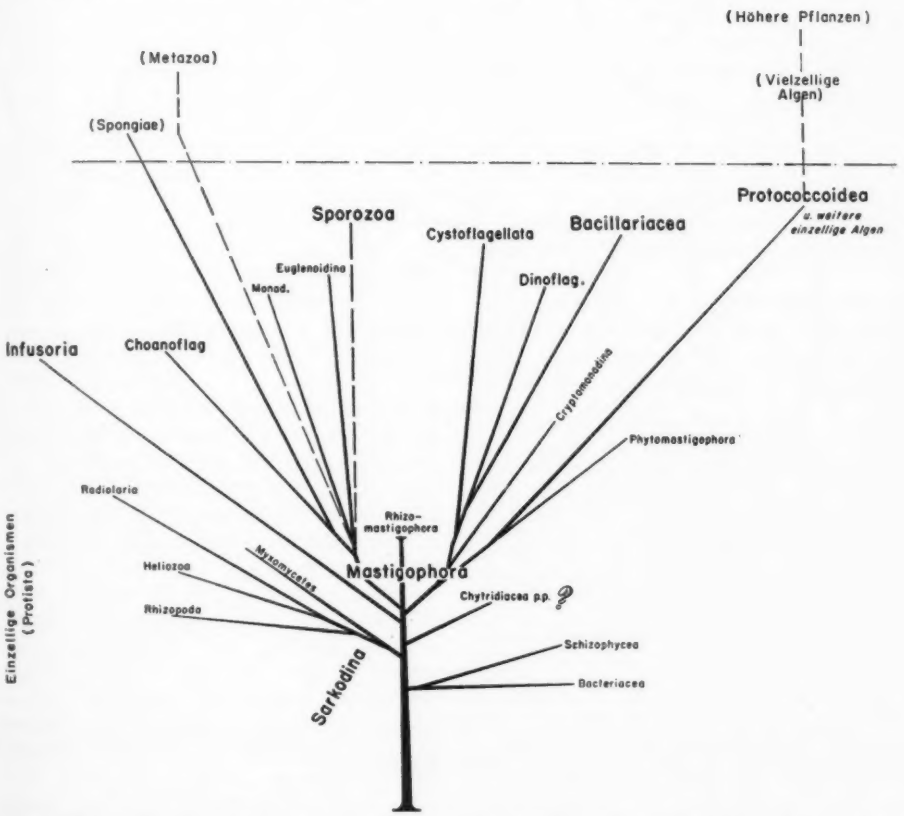

PLATE III. A redrawing of Bütschli's (1880) phylogenetic tree for the Protozoa and forms presumably closely related to them. Note the four protozoan classes: Sarkodina, Mastigophora, Sporozoa, and Infusoria. (Bütschli's groups "Rhizomastigoda" and "Phytomastigoda" are inadvertently labelled "Rhizomastigophora" and "Phytomastigophora" here.)

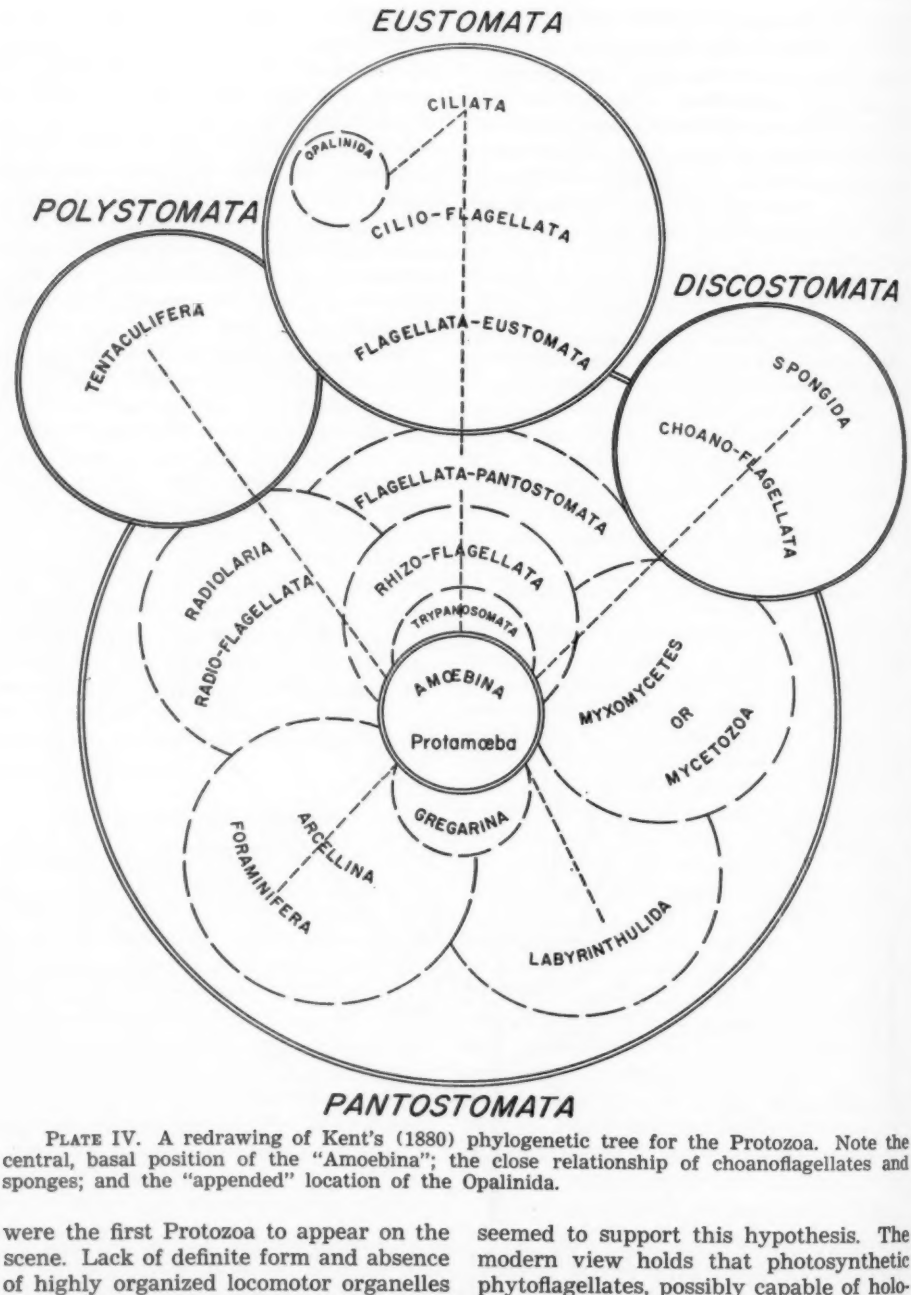

PLATE IV. A redrawing of Kent's (1880) phylogenetic tree for the Protozoa. Note the central, basal position of the "Amoebina"; the close relationship of choanoflagellates and sponges; and the "appended" location of the Opalinida.

were the first Protozoa to appear on the scene. Lack of definite form and absence of highly organized locomotor organelles and elaborate cytoplasmic structures seemed to support this hypothesis. The modern view holds that photosynthetic phytoflagellates, possibly capable of holozoic nutrition as well, were probably an-

cestral not only to the Protozoa proper but also to the entire plant and animal kingdoms. Present-day forms which may closely resemble such a primitive protozoan may be found in the order Chrysomonadida, according to some workers; in the order Cryptomonadida, according to others. Analyses of pigments are particularly important here, a subject far beyond the scope of the present paper (see such works as Hutner and Provasoli, 1951; Dougherty, 1955; Dougherty and Allen, 1959).

Higher plant life, as well as various algae and the Phytomastigophora, are quite easily derived, in a broad way, from primitive pigmented flagellates. The Zoomastigophora represent a more troublesome group, although the postulation of loss of the photosynthetic ability concomitant with increase of organellar complexity is not a difficult one to make. The free-living "lower" zooflagellates, the blood parasites, and the complex symbiotic forms (Pl. V) represent groups presumably separated by many mutations of adaptive value and by long spans of time. Kirby (1947, 1949a, b) has offered comprehensive treatments of some of the complicated problems involving zooflagellate interrelationships.

The curious choanoflagellates have been considered progenitors of the Parazoa or sponges by a number of systematists because of the characteristic collar cells present in both groups of organisms. The important, rather rare form described by Kent 80 years ago and named *Proterospongia* (see Pl. I, Fig. 7) has been the center of considerable controversy. On the one hand, it has been hailed as a "missing link" organism. On the other hand, it has been discounted as a fragment of a sponge, thus committing it to the receptive realm of protozoan mythology. The extensive work on sponges by Duboscq and Tuzet (1937) and Tuzet (1945) has been responsible for the latter attitude. In very recent years, however, the existence of the flagellate has been confirmed in scattered rediscoveries (Schiller, 1953; Grøntved, 1956; Lackey, 1959). It seems to me that the hypothesis of sponge origin from ancestral forms of such present-day choanoflagellates is a very reasonable one. In agreement with Hyman (1940) and many others, however, and in strong disagreement with Copeland (1956), I do not consider the sponges on the main line of evolutionary origin of the Eumetazoa.

The opalinids may be considered to have arisen from fairly complex zooflagellate stock (see Pl. V), possibly not far from the postulated branch leading to the ciliate assemblage. Certain features possessed in common by these aberrant flagellates and the ciliates might thus be explained; parallel evolution may be a factor as well.

Back near the base of the main trunk of our tree (Pl. V), the "Sarcodina" [7] probably arose in very ancient times. Conceivably the fungi, at least of the mycetozoan group, had their origins from the same zooflagellate-derived branch which leads to the present-day rhizopods and actinopods.

The Sporozoa and Cnidosporidia are generally supposed to have had a zooflagellate or amoeboflagellate ancestry. In the case of the enigmatic cnidosporidian

[7] In the tree presented in Plate V, I have used the conventional subdivisions of the phylum into five groups of not quite equal rank: the Phytomastigophora, the Zoomastigophora, the Sarcodina, the Sporozoa, the Ciliophora. To prevent possible confusion, I should point out clearly that these convenient "tree groupings" fall into the following subphyla as recognized by me in the text of this paper: the Phytomastigophora and Zoomastigophora are subclasses of the class Flagellata in the superclass Rhizoflagellata belonging to subphylum I, the MASTIGAMOEBAEA; the "Sarcodina" of the tree embraces the class Rhizopoda of the same superclass Rhizoflagellata, and also members of the related superclass Actinopoda of the same subphylum. The term "Sporozoa" includes both subphylum II, the SPOROZOA, and subphylum III, the CNIDOSPORIDIA, as these groups are delineated in the text. The label Ciliophora represents subphylum IV, the CILIOPHORA, without change.

group there is scarcely any evidence in support of the assumption, as many authors have readily admitted. In fact, some biologists have suggested that cnidosporidians represent degenerate Metazoa. Part of the difficulty in attempting to trace phylogenetic relationships involving these Protozoa is their totally parasitic mode of life; in what form they or their immediate ancestors existed before the arrival of their hosts on this earth is a matter of purest conjecture. Evolutionary trends *within* certain of the ordinal groups have been postulated from time to time by various workers (e.g., see the very recent paper on the Myxosporidiida by Shulman, 1959). There is no reason other than practical convenience for considering the Sporozoa and the Cnidosporidia as closely related groups of species. Thus the proximity of their origins as depicted in the tree (Pl. V) has no real factual basis.

The Ciliophora very likely arose from a zooflagellate line; when and where nobody knows. Minchin (1912), and others before and since him, have reached the same conclusion after more or less extensive discussion of the frustrating problem. Modern comparative studies have served as a basis for several hypotheses regarding interrelationships among the several main groups. A special ciliate tree appears in Plate II; the position of the several orders has had to be simplified in the phylum tree (Pl. V). It should be recalled that the infraciliature is considered a more fundamental property of ciliates than their external ciliature (Corliss, 1956, 1959a). Although the Ciliophora are divided into two major groups, the Holotricha and the Spirotricha, the latter more compact and smaller group is postulated to have arisen from an "intermediate" order of the former. Subsequent radiation within the spirotrich group, accompanied by an intensification of characteristics not present in holotrichs, appears to justify the taxonomic separation even if it does not reflect the supposed phylogeny perfectly (see Pl. V). Parallels for such a systematic conclusion are found among metazoan groups, even the vertebrates.

Origin of Metazoa from Protozoa

One further aspect of the protozoan tree remains for brief discussion. If Metazoa arose from the phylum Protozoa, which protozoan group is directly implicated in this most important evolutionary step? Whether Protozoa are considered unicellular or acellular,[8] there is practically universal agreement among biologists that they must have served as the source from which the Eumetazoa arose. Intimately involved, then, is this further question: which eumetazoan group, if represented at all among present-day forms, was the first to establish multicellularity as an enduring way of life?

Reasonable candidates for the answer to the first question include the phytoflagellates and the most primitive ciliates; the rhizopod "slime mold" groups, possibly with justification, are seldom considered to be ancestral to any "higher" groups other than fungi. As for the most primitive eumetazoan taxon, the hydrozoan cnidarians and the acoel turbellarians appear to be the main contenders for the title.

Hyman (1940) has offered a scholarly review of the over-all problem to which the reader is referred. Hyman herself supports what may be considered a neo-Haeckelian viewpoint. This popular hypothesis emphasizes the possibility of transformation of a *Volvox*-like ancestor into a parenchymula or stereogastrula, a

[8] I still cannot agree with the conclusions of Hyman (1940, 1959) who supports the acellularity concept of Dobell (1911) so adamantly. The controversy seems to revolve around this question: can (or cannot) Protozoa *function* as the "complete organisms" that they obviously are and still be "cells" in their *morphology*, possessing as they do certain basic structural homologies with metazoan cells? I have treated this subject very briefly elsewhere (Corliss, 1957b); I regret that further discussion here would be beyond the scope of the present paper.

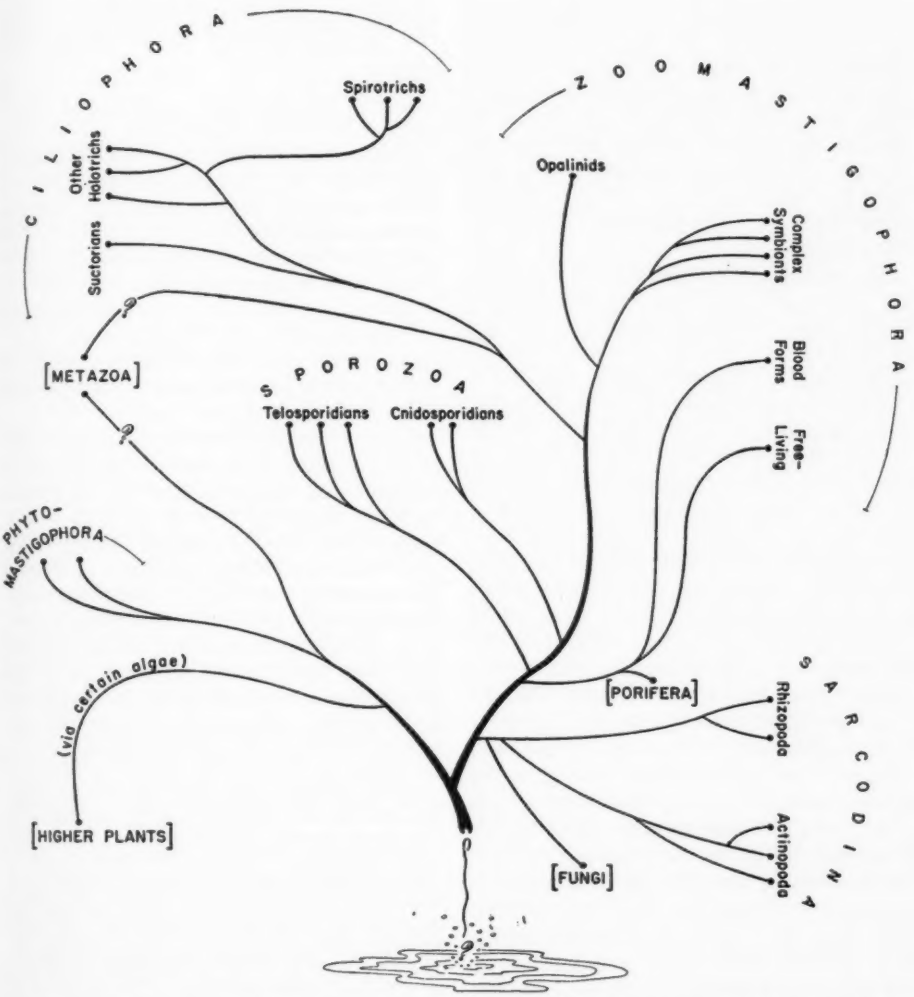

PLATE V. A proposed phylogenetic tree for the phylum PROTOZOA. Primitive phytoflagellates presumably were the first Protozoa, serving as the direct ancestors of the two major lines of flagellates well-known today. Early in the development of the zooflagellate line the amoeboid Protozoa are supposed to have branched off to form their own special lines of phylogeny. "Sporozoan" groups allegedly have a fairly primitive flagellate ancestry also. The ciliates are generally thought to have arisen from the flagellate line at a quite highly developed level. Origin of the Metazoa may have been from a colonial phytoflagellate line *or* from a primitive ciliate-type of protozoan. See text for discussion of the major features of this obviously simplified, dendrogrammatic representation of the supposed phylogeny of a group of organisms whose real phylogeny can never be known for certain. (Please note that the group names which appear here in capital letters are those of the conventional protozoological literature. Their relationship to the somewhat modified taxonomic groupings endorsed in the present paper is explained in footnote 7.)

form characteristic of present-day cnidarian (coelenterate) larvae. Very recently Hyman (1959) has taken the opportunity of bringing her discussion on the subject up-to-date. She has found no reason to change the essence of her earlier comments; and she leaves the reader with this sobering advice, that "such phylogenetic questions . . . [are] insoluble on present information."

Too recent, unfortunately, for the latest review by Hyman was the provocative, well-documented essay by Hanson (1958). Hanson supports a somewhat refined form of the Hadži (1953; and earlier papers not cited here) hypothesis. Hadži has proposed that the most primitive eumetazoan was an Acoela-like turbellarian and that it evolved from a polyenergid ciliate-like protistan form. Hanson, who offers a clear-cut summary of his own ideas in a phylogenetic tree which depicts the position of a number of protozoan groups, stresses the "differentiation of energid heterogeneity," relegating cells to a role of secondary importance in the evolutionary sequence from "physiologically *compound* polyenergid" forms to "physiologically *complex* polyenergid" forms. His scheme starts with a hypothetical multinucleate, akaryomastigont flagellate which gives rise to a hypothetical protociliate. From this latter form the Acoela, on the one hand, and the Ciliophora proper, on the other, originate, proceeding immediately along sharply diverging evolutionary lines of their own.

Further discussion of these two hypotheses, the integration of a protozoan colony (broadly the Colonial Theory) and the compartmentalization of an individual protozoan (essentially the Syncytial Theory), is inappropriate here. Suffice it to say that there are serious weaknesses in both of them: a most frustrating situation! The two possible evolutionary paths are included, each with a prominent question mark, in the tree (Pl. V). Major though the problem is, it is surely tantalizingly [9] unanswerable, since the crucial facts in the case will never be available.

Summary and Conclusions

Because of the nature of their material, systematic protozoologists are greatly handicapped in determining phylogenetic interrelationships. It follows that "natural" classification schemes of the Protozoa suffer for the same reasons. The outlook is not bright. As new techniques of study are developed, however, and as new data accrue and new hypotheses are promulgated, we may expect some improvement over existing systems.

The "Phylum PROTOZOA" is probably here to stay, as a matter of practical convenience and because of long-time popular usage, if for no other reasons. Distribution of its present membership into several different phyla scattered throughout an unfamiliar (both in name and content) "kingdom" seems premature, particularly in view of our tremendous lack of knowledge concerning the actual interrelationships of the many diverse groups involved. Enough problems remain at levels below the phylum.

[9] There are a number of fascinating parallels among odd structures found in both certain Protozoa and certain Metazoa. Although these are probably of no phylogenetic significance, it may be interesting to mention a few specific cases: the ultrastructural similarity between the phytoflagellate eyespot and the external segment of a vertebrate visual cell (Fauré-Fremiet, 1958b); the possible identity of a dinoflagellate pigment with one isolated from certain sea anemones (Hall, 1953; Heilbron et al., 1935); the presence of nematocysts in certain dinoflagellates, trichocysts in some flagellates and many ciliates, and polar filaments in cnidosporidians, reminding one of the cnidarian nematocyst (Picken, 1953); the occurrence, in a number of gymnostome ciliates, of vesicles or vacuoles of some complexity considered by various workers as statocysts comparable to those of certain molluscs and crustaceans (Hall, 1953; Kudo, 1954); the remarkable octoradial planktonic gymnostome ciliate(?) suggestive of a cnidarian medusa and a ctenophore (Weill, 1946).

The "Sarcodina-Mastigophora" problem calls for a fairly major revision of conventional schemes of classification in several areas. Mainly following leads suggested by others, I have proposed recognition of a subphylum MASTIGAMOEBAEA to contain three superclasses: the Rhizoflagellata (with classes Flagellata and Rhizopoda), the Actinopoda, and the Paraflagellata (for the opalinids). Revolutionary changes are not envisioned at the class or ordinal levels within these groups.

The "Mycetozoa" probably should be returned *in toto* to the mycologists, even though a protozoan ancestry seems a reasonable assumption. The "Acrasiales" might be retained in the phylum Protozoa as a group of uncertain taxonomic status appended to the Rhizopoda.

The position of the opalinids remains enigmatic. Possible affinities with both flagellates and ciliates are complicated by their symbiotic existence and their presumably long evolutionary history apart from any other protozoan group. Whether the Opalinida are included as aberrant forms within the subphylum Mastigamoebaea or as a special group appended to the subphylum Ciliophora probably makes little difference at the present stage of our knowledge. For the time being, I favor the former allocation.

At least a major part of the stigma of the accusation that they represent a polyphyletic assemblage of forms is removed from the "Sporozoa" if they are recognized as comprising two principal groups of high and equal rank. Thus I urge realistic acceptance of a subphylum SPOROZOA (for the Telosporidia of the literature) and a separate subphylum CNIDOSPORIDIA. The Sarcosporidia may well be fungi of some sort; more facts are needed before a firm decision can be made concerning their most reasonable taxonomic position.

Problems within the fourth and last subphylum of Protozoa, the CILIOPHORA, do not seem quite as unresolvable as some of those presented by the other groups. Recent revisions suggested by Fauré-Fremiet have been endorsed, with slight modification, by the writer. The major features of the new ciliate classification scheme have been discussed briefly in the present paper. These include: total exclusion of the "protociliates" (the opalinids) from the subphylum; incorporation of the chonotrichs, peritrichs, and suctorians as orders of the subclass Holotricha; retention of the smaller subclass Spirotricha to contain several orders characterized by possession of more conspicuously developed compound ciliary organelles.

In spite of the necessarily speculative nature of any protozoan phylogenetic tree, one is presented in this paper—the first published since 1880. Although inadequate to illustrate precisely even the factual data which are available, it can serve as a convenient basis for discussion of possible phylogenetic relationships within and beyond the phylum boundaries. A problem of considerable interest to the invertebrate systematist is that of the origin of the Metazoa from the Protozoa. The sponges appear to have had an ancestry among the choanoflagellates. But the Eumetazoa may have arisen from either a colonial phytoflagellate of some sort or a ciliate-like progenitor, according to the two principal theories concerning their origin. The primitive eumetazoan is postulated to have been a hydrozoan cnidarian in the first case, an acoel turbellarian in the second. There are, seemingly, sound arguments and serious weaknesses on both sides of this tantalizing question which, in the last analysis, is quite unanswerable.

REFERENCES

ALLEN, M. B., DOUGHERTY, E. C., and MCLAUGHLIN, J. J. A. 1959. Chromoprotein pigments of some cryptomonad flagellates. Nature, 184:1047–1049.

BADER, R. S. 1958. Similarity and recency of common ancestry. Syst. Zool., 7:184–187.

BALL, G. H. 1960. Some considerations regarding the Sporozoa. Jour. Protozool., 7: 1–6.

BIGELOW, R. S. 1958. Classification and phylogeny. Syst. Zool., 7:49–59.

BIOCCA, E. 1956. Alcune considerazioni sulla sistematica dei protozoi e sulla utilità di creare una nuova classe di protozoi. Rev. Brasil. Malariol. Doenc. Trop., 8:91–102. [In Italian with brief Eng., Fr., and Portug. summ.]

——— 1958. Essai de classification de *Toxoplasma, Sarcocystis,* et organismes voisins. Cesk. Parasitol., 5:37–44.

BONNER, J. T. 1959. The cellular slime molds. Princeton Univ. Press, Princeton, New Jersey.

BRADFIELD, J. R. G. 1955. Fibre patterns in animal flagella and cilia. Symposia Soc. Exptl. Biol., 9:306–334.

BRENT, M. M. 1957. Flagellate-to-amoeba transformation induced in *Tetramitus rostratus* by nitrogen mustard. Nature, 179–1029.

BÜTSCHLI, O. 1880–1889. Sarkodina und Sporozoa . . . (Abt. I, 1880–1882); Mastigophora (Abt. II, 1883–1887); Infusoria und System der Radiolaria (Abt. III, 1887–1889). *In:* BRONN, H. G., Klassen und Ordnung des Thier-Reichs, 1:1–2035. C. F. Winter, Leipzig.

——— 1880. [Page xii of Abt. I (see above reference)]

CALKINS, G. N. 1933. The biology of the Protozoa. 2 ed. Lea and Febiger, Philadelphia.

CHEN, T. T. 1948. Chromosomes in Opalinidae (Protozoa, Ciliata) with special reference to their behavior, morphology, individuality, diploidy, haploidy, and association with nucleoli. Jour. Morphol., 83:281–359.

COPELAND, H. F. 1956. The classification of lower organisms. Pacific Books, Palo Alto, California.

CORLISS, J. O. 1955. The opalinid infusorians: flagellates or ciliates? Jour. Protozool., 2:107–114.

——— 1956. On the evolution and systematics of ciliated Protozoa. Syst. Zool., 5:68–91, 121–140.

——— 1957a. Nomenclatural history of the higher taxa in the subphylum Ciliophora. Arch. Protistenk. 102:113–146.

——— 1957b. Concerning the "cellularity" or acellularity of the protozoa. Science, 125: 988–989.

——— 1958. The phylogenetic significance of the genus *Pseudomicrothorax* in the evolution of holotrichous ciliates. Acta Biol. Acad. Sci. Hungarica, 8:367–388.

——— 1959a. Some basic problems in the study of evolution of the ciliated Protozoa. Proc. XV Intern. Congr. Zool., London, 1958:179–182.

——— 1959b. An illustrated key to the higher groups of the ciliated Protozoa, with definition of terms. Jour. Protozool., 6:265–281.

——— 1960. The problem of homonyms among generic names of ciliated Protozoa, with proposal of several new names. Jour. Protozool., 7. (In press.)

DEDEKEN-GRENSON, M. 1959. The mass induction of white strains in *Euglena* as influenced by the physiological conditions. Exptl. Cell Research, 18:185–187.

DENNIS, E. W. 1930. The morphology and binary fission of *Babesia bigemina* of Texas cattle-fever. Univ. California Publ. Zool., 33:179–192.

——— 1932. The life-cycle of *Babesia bigemina* (Smith and Kilbourne) of Texas cattle-fever in the tick *Margaropus annulatus* (Say) with notes on the embryology of *Margaropus*. Univ. California Publ. Zool., 36:263–298.

DEVIDÉ, Z. 1951. Chromosomes in ciliates (Euciliata and Opalinidae). Bull. Intern. Acad. Yougoslave (N. S.), 3:75–114.

DOBELL, C. 1911. The principles of protistology. Arch. Protistenk., 23:269–310.

——— 1940. Researches on the intestinal Protozoa of monkeys and man. X. The life-history of *Dientamoeba fragilis:* observations, experiments, and speculations. Parasitology, 32:417–461.

DOFLEIN, F. and REICHENOW, E. 1927–1929. Lehrbuch der Protozoenkunde. 5 ed. G. Fischer, Jena.

——— 1949–1953. Lehrbuch der Protozoenkunde. 6 ed. G. Fischer, Jena.

DOUGHERTY, E. C. 1955. Comparative evolution and the origin of sexuality. Syst. Zool., 4:145-169, 190.

DOUGHERTY, E. C., and ALLEN, M. B. 1959. Speculations on the position of the cryptomonads in protistan phylogeny. Proc. XV Intern. Congr. Zool., London, 1958: 184–186.

DUBOSCQ, O. and TUZET, O. 1937. L'ovogénèse, la fécondation et les premiers stades du développement des éponges calcaires. Arch. Zool. Exptl. Gén., 79:157–316.

EHRET, C. F. and POWERS, E. L. 1959. The cell surface of *Paramecium*. Intern. Rev. Cytol., 8:97–133.

FAURÉ-FREMIET, E. 1950. Morphologie comparée et systématique des ciliés. Bull. Soc. Zool. France, 75:109–122.

——— 1957a. Finer morphology of microorganisms. Ann. Rev. Microbiol., 11:1–6.

——— 1957b. Le macronucleus hétéromère de quelques ciliés. Jour. Protozool., 4:7–17.

——— 1958a. Structure et ultrastructure des protistes. Rev. Pathol. Gén. Physiol. Clin., No. 695:265–279.

——— 1958b. The origin of the Metazoa and the stigma of the phytoflagellates. Quart. Jour. Microsc. Sci., 99:123–129.

Fauré-Fremiet, E., Rouiller, C., and Gauchery, M. 1956. Structure et origine du péduncule chez *Chilodochona*. Jour. Protozool., 3:188–193.

Finley, H. E., McLaughlin, D., and Harrison, D. M. 1959. Non-axenic and axenic growth of *Vorticella microstoma*. Jour. Protozool., 6:201–205.

Grassé, P. P. (ed.) 1952. Traité de Zoologie. Anatomie, Systématique, Biologie. Vol. I, fasc. 1. Phylogénie. Protozoaires: Généralités, Flagellés. Masson and Cie, Paris.

——— 1953. Traité de Zoologie. Anatomie, Systématique, Biologie. Vol. I, fasc. 2. Protozoaires: Rhizopodes, Actinopodes, Sporozoaires, Cnidosporidies. Masson and Cie, Paris.

Grøntved, J. 1956. Planktological contributions. II. Taxonomical studies in some Danish coastal localities. Meddel. Danmarks Fiskeri-og Havundersøg., N.S. 1:No. 12.

Guilcher, Y. 1951. Contribution à l'étude des ciliés gemmipares, chonotriches et tentaculifères. Ann. Sci. Natur. Zool., ser. 11, vol. 13:33–132.

Hadži, J. 1953. An attempt to reconstruct the system of animal classification. Syst. Zool., 2:145–154.

Hall, R. P. 1953. Protozoology. Prentice-Hall, New York.

Hanson, E. D. 1958. On the origin of the Eumetazoa. Syst. Zool., 7:16–47.

Haxo, F. T. and Fork, D. C. 1959. Photosynthetically active accessory pigments of cryptomonads. Nature, 184:1051–1052.

Heilbron, I. M., Jackson, H., and Jones, R. N. 1935. The lipochromes of sea anemones. I. Carotenoid pigments of *Actinia equina, Anemonia sulcata, Actinoloba dianthus* and *Tealia felina*. Biochem. Jour. 29:1384–1388.

Hutner, S. H. and Provasoli, L. 1951. The phytoflagellates. *In:* Lwoff, A. (ed.). Biochemistry and physiology of Protozoa. Vol. I: 27–188. Academic Press, New York.

Hyman, L. H. 1940. The invertebrates. Vol. I. Protozoa through Ctenophora. McGraw-Hill, New York.

——— 1959. The invertebrates. Vol. V. Smaller coelomate groups. McGraw-Hill, New York.

Jahn, T. L. and Jahn, F. F. 1949. How to know the Protozoa. Brown, Dubuque, Iowa.

Jahn, T. L. and Rinaldi, R. A. 1959. Protoplasmic movement in the foraminiferan, *Allogromia laticollaris;* and a theory of its mechanism. Biol. Bull., 117:100–118.

Jírovic, O., Wenig, K., Fott, B., Bartoš, E., Weiser, J., and Šrámek-Hušek, R. 1953. Protozoologie. Prague. [In Czechoslovakian.]

Kahl, A. 1930–1935. Urtiere oder Protozoa. I: Wimpertiere oder Ciliata (Infusoria), eine Bearbeitung der freilebenden und ectocommensalen Infusorien der Erde, unter Ausschluss der marinen Tintinnidae. *In:* Dahl, F. (ed.). Die Tierwelt Deutschlands, Parts 18 (1930), 21 (1931), 25 (1932), 30 (1935). G. Fischer, Jena.

——— 1931. Über die verwandtschaftlichen Beziehungen der Suctorien zu den prostomen Infusorien. Arch. Protistenk., 73:423–481.

Kent, W. S. 1880–1882. A manual of the Infusoria. Vols. I–III. David Bogue, London (see p. 37).

Kirby, H. 1946. *Gigantomonas herculea* Dogiel, a polymastigote flagellate with flagellated and amoeboid phases of development. Univ. California Publ. Zool., 53:163–226.

——— 1947. Flagellate and host relationships of trichomonad flagellates. Jour. Parasitol., 33:214–228.

——— 1949a. Morphology, morphogeny and kinship in some nonpigmented Flagellata. C.R. XIII Congr. Intern. Zool., Paris, 1948: 191–194.

——— 1949b. Systematic differentiation and evolution of flagellates in termites. Rev. Soc. Mexicana Hist. Natur., 10:57–79.

Kudo, R. R. 1954. Protozoology. 4 ed. Thomas, Springfield, Illinois.

Lackey, J. B. 1959. Morphology and biology of a species of *Protospongia*. Trans. Amer. Microsc. Soc., 78:202–206.

Macbride, T. H. and Martin, G. W. 1934. The Myxomycetes. Macmillan, New York.

Madison, K. M. 1958. Fossil protozoans from the Keewatin sediments. Trans. Illinois State Acad. Sci., 50:287–290.

Minchin, E. A. 1912. An introduction to the study of the Protozoa. Edward Arnold, London.

Mohr, J. L. 1959. M. M. Metcalf and the significance of opalinid distribution. (Abstr.) Jour. Protozool., 6(Suppl.):13.

Noirot-Timothée, C. 1958. Quelques particularités de l'ultrastructure d'*Opalina ranarum* (Protozoa, Flagellata). C. R. Acad. Sci., Paris, 247:2445–2447.

Noland, L. E. 1957. Protoplasmic streaming: a perennial puzzle. Jour. Protozool., 4:1–6.

ÓhEocha, C. and Raftery, M. 1959. Phycoerythrins and phycocyanins of cryptomonads. Nature, 184:1049–1051.

Picken, L. E. R. 1953. A note on the nematocysts of *Corynactis viridis*. Quart. Jour. Microsc. Sci., 94:203-227.

Piekarski, G. 1954. Lehrbuch der Parasitologie. Springer, Berlin.

Pitelka, D. R. 1956. An electron microscope study of cortical structures of *Opalina ob-*

trigonoidea. Jour. Biophys. Biochem. Cytol., 2:423–432.

——— 1959. Comparative morphology of the ciliary apparatus. Proc. XV Intern. Congr. Zool., London, 1958:473–475.

PITELKA, D. R. and SCHOOLEY, C. N. 1955. Comparative morphology of some protistan flagella. Univ. California Publ. Zool., 61: 79–128.

POCHE, F. 1913. Das System der Protozoa. Arch. Protistenk., 30:125–321.

PRINGSHEIM, E. G. 1948. The loss of chromatophores in *Euglena gracilis*. New Phytologist, 47:52–68, 79–87.

PUYTORAC, P. DE. 1954. Contribution à l'étude cytologique et taxonomique des infusoires astomes. Ann. Sci. Natur., Zool., ser. 11, vol. 16:85–270.

——— 1959. Quelques observations sur l'évolution et les origines des ciliés Astomatida. Proc. XV Intern. Congr. Zool., London, 1958:649–651.

RAABE, Z. 1958. An attempt of a revision of the system of Protozoa. Ann. Univ. M. Curie-Skłodowska, Sect. C, 3:259–276. [In Polish with Eng. summ.]

RAIKOV, I. B. 1958. Der Formwechsel des Kernapparates einiger niederer Ciliaten. I. Die Gattung *Trachelocerca*. Arch. Protistenk., 103:129–192.

ROTH, L. E. 1957. An electron-microscope study of the cytology of the protozoan *Euplotes patella*. Jour. Biophys. Biochem. Cytol., 3:985–1000.

——— 1959. An electron-microscope study of the cytology of the protozoan *Peranema trichophorum*. Jour. Protozool., 6:107–116.

SCHILLER, J. 1953. Über neue Craspedomonaden (Choanoflagellaten). Arch. Hydrobiol., 48:248–259.

SHULMAN, S. S. 1959. The main direction of evolution in the order Myxosporidia. Zool. Zhurnal, 38:1481–1497. [In Russian with English summary.]

SPARROW, F. K. 1958. Interrelationships and phylogeny of the aquatic Phycomycetes. Mycologia, 50:797–813.

SPINDLER, L. A. 1947. A note on the fungoid nature of certain internal structures of Miescher's sacs (*Sarcocystis*) from a naturally infected sheep and a naturally infected duck. Proc. Helminthol. Soc. Washington, 14:28–30.

SPINDLER, L. A., and ZIMMERMAN, H. E., JR. 1945. The biological status of *Sarcocystis*. (Abstr.) Jour. Parasitol., 31 (Suppl.): 13.

STEIN, F. 1867. Der Organismus der Infusionsthiere nach eigenen Forschungen in systematischer Reihenfolge bearbeitet. II. Leipzig.

TUFFRAU, M. 1953. Les processus cytologiques de la conjugaison chez *Spirochona gemmipara* Stein. Bull. Biol. France Belgique, 87: 314–322.

TUZET, O. 1945. Sur les agrègats de choanocytes et la question de la *Proterospongia* avec quelques remarques sur les réseaux formés par les cellules dissociées. Arch. Zool. Exptl. Gén., 84:225–238.

ULRICH, W. 1950. Begriff und Einteilung der Protozoen. *In* Moderne Biologie, Festschrift zum 60 Geburtstag von Hans Nachtsheim, Berlin: 241–250.

WEILL, R. 1946. *Ctenoctophrys chattoni* n. g. n. sp., infusoire planctonique octoradié, à caractère de méduse et de cténophore. C. R. Acad. Sci., Paris, 222:683–685.

WENRICH, D. H. 1944. Nuclear structure and nuclear division in *Dientamoeba fragilis* (Protozoa). Jour. Morphol., 74:467–491.

WENYON, C. M. 1926. Protozoology, a manual for medical men, veterinarians and zoologists. 2 Vols. Ballière, Tindall and Cox, London.

WESSENBERG, H. 1957. Studies on the life cycle and morphogenesis of *Opalina*. (Abstr.) Jour. Protozool., 4(Suppl.):13.

WHITTAKER, R. H. 1959. On the broad classification of organisms. Quart. Rev. Biol., 34: 210–226.

YANG, W. C. T. 1960. On the continuous culture of opalinids. Jour. Parasitol., 46:32.

JOHN O. CORLISS is Associate Professor of Zoology at the University of Illinois and has become a leader in the study of the ciliate Protozoa. He gratefully acknowledges assistance from a National Science Foundation grant and the artistic assistance of Miss Alice Boatright and Mr. Charles H. Beiger, Jr., in the preparation of the plates.

On the Origin and Phylogeny of the Coelenterates[1]

CADET HAND

IN the last few years an intriguing argument has developed concerning the origin and phylogeny of the coelenterates, or more properly, the Cnidaria. The argument, in its simplest form, consists of two quite opposite views which hold that on the one hand the Hydrozoa are the more ancient class of the phylum while the other argues for the Anthozoa as the more ancient. This latter view stems from the work of Hadzi (1944, 1953), while the opposing view is an older one and is discussed, championed, and extended by Hyman (1940, 1959). The more traditional viewpoint, that of Hyman, holds that the ancestral cnidarian was a primitive medusa which developed from a planula to an actinula. The actinula at some time evolved the habit of budding other actinulae before its own metamorphosis to the medusa. This habit of budding established the hydroid phase as we know it today. In this theory the pre-cnidarian is held to have been a gastraea type of organism, polarized and free-swimming. Hyman (1940, p. 634) further suggests that the gastrea went on to a hypothetical stage which she pictures as being ". . . a small rounded bottom-feeding organism with a ciliated surface, mouth, archenteron, and aboral sense organ. There were probably some mesenchyme cells of ectodermal origin between ectoderm and entoderm, and the archenteron may have had lateral pockets in which the sex cells ripened. Such a hypothetical organism has been named by Naef a metagastraea." This theory may be called the *medusa theory* and accepts the radial symmetry of the cnidarians as a basic and primitive character.

The opposing point of view to the medusa theory is the *turbellarian theory* as developed by Hadzi. He holds that the primitive cnidarian was an anthozoan polyp, derived ancestrally from a rhabdocoel turbellarian. This derivation assumes that a flatworm became sessile and developed the features of the anthozoan polyp. Thus the bilaterality seen in anthozoan polyps would be a primitive and basic cnidarian feature. Radiality would be a secondarily developed character derived as a by-product of the sessile habit. Jägersten (1955) and Marcus (1958) both accept the Anthozoa as the most primitive of the Cnidaria, although neither adds new factual material to the general theory.

It is the purpose of this paper to assess these two contrasting theories to see if a marshalling of the data can lead us to a conclusion that one or the other can better be accepted. It is not my intention to delve into the question of the origin of the Metazoa nor to assess in detail all of the phylogenetic speculations set forth by any of the afore-mentioned authors. Our question is, *"Is radiality or bilaterality the more primitive symmetry of the Cnidaria and, as a corollary, is the tetramerous medusa or a bilateral polyp the more ancestral body form?"* Like Carter (1954, p. 163) I hope that it will be ". . . on a *balance* of all the evidence, whether old or new, that we should [will] found our conclusions."

With this brief introduction it is time now to examine our theories in detail.

[1] Dr. Hand was unable to be present in person. Dr. M. J. Greenberg of the zoology department of the University of Illinois kindly consented to read his paper.

There is one interesting similarity between them, namely the general agreement that the pre-cnidarian was planula-like. Beyond this the theories diverge completely. That the planula as a larva is basic to the Cnidaria is readily acceptable and that a planuloid organism may have been ancestral to both flatworms and cnidarians seems reasonable. These conclusions unfortunately do not tell us which came first, the Cnidaria or Platyhelminthes, however, and so do not help us solve the problem at hand.

The question, which seems most in need of resolution, is what was the original or primitive symmetry of the Cnidaria. If we could answer this we could take some stand on the phylogeny of the group. Actually part of what we are trying to answer is more fundamental than our immediate question. What we are seeking an answer to is whether the Radiata (Cnidaria and Ctenophora) is a valid evolutionary concept; that is, is radial symmetry more ancient of itself than bilateral symmetry?

Radial symmetry is clearly referable to a sessile way of life. The radiality of echinoderms or of acorn barnacles seems best explained in this way. We could also point to the radial arrangement of the tentacles of such sessile groups as entoprocts, ectoprocts, some polychaetes, and phoronids as further evidence that our generalization is valid. Using these groups as evidence the contention that the radial symmetry of the Cnidaria could be derived from sessility is admissible. This, of course, is an important part of the turbellarian theory. However, the admission of the association of radial symmetry and a sessile way of life does not necessarily prove that the Cnidaria have been derived from sessile ancestors. I think the possibility must still be admitted that radial symmetry can have other origins as I will now try to show.

The early development of many organisms takes place in an aqueous environment. Sometimes eggs are spawned freely into the surrounding water and sometimes each egg or a few eggs are confined in a capsule or a gelatinous envelope. The point is that cleavage and early development in many organisms takes place in an environment that impinges on all sides. For many marine organisms the environment is that of open waters and the developing individual is in fact planktonic. This particular habitat may well be the ancestral one of Metazoa, and the radial symmetry exemplified by most cleaving embryos through the time of their gastrulation may be related to their planktonic development. I think there is no argument that in general the stages of embryos up to the gastrula are radial, and that it is only in the later stages that this radial symmetry is lost. Therefore I hope we can agree that it is possible that radial symmetry could be primitive in the evolution of the Metazoa and that it could come from sources other than adaptations to a sessile existence.

In the foregoing I stressed the planktonic way of life as being a factor in the development of radial symmetry. Let us explore this further. The Protozoa as a non-metazoan group may be worth looking at critically. Body form in this group must be susceptible to the same evolutionary changes and selective forces as in the Metazoa, but we do not have to be concerned about differences between their embryonic and adult symmetries. Thinking only of the non-parasitic species we can identify spherically, radially, and bilaterally symmetrical forms. As in the Metazoa, many sessile forms are radial. Among the completely free-floating, non-motile forms we find the spherically or radially symmetrical Radiolaria. Some flagellates, foraminiferans, and ciliates are radially symmetrical too. Bilateral symmetry is closely approximated in many creeping ciliates. It is my contention that the radial symmetry seen in the free-floating and weakly swimming forms is the expression of selective forces which tend to lead to radial symmetry in these organ-

isms, just as a creeping existence seems to lead to bilaterality. So far I hope I have established that radial symmetry may be primitive on purely embryological grounds, and that, as well as being related to a sessile existence, it may also result from a free-floating or very feebly swimming way of life.

The only satisfactory examples of radially symmetrical and planktonic metazoans which we can readily cite are to be found among the Cnidaria and Ctenophora. Superficially some rotifers, some trochophores, and other larvae also fit our requirements. Why, one asks, if a planktonic existence is conducive to evolution toward radiality, are not radially symmetrical plankters more common? I believe the answer is that all planktonic organisms at evolutionary levels higher than the coelenterates are derived from bilateral ancestors. This, plus their stronger swimming powers, has made the retention of bilaterality of greater advantage than a secondary change to radiality. I think, too, that the absence of change of body form of such radially symmetrical plankters as the planktonic sea cucumber *Pelagothuria*, the sea anemone *Minyas*, the colonial hydroid *Velella* or *Porpita*, or the colony form of many of the floating siphonophores argues for radiality as being an acceptable and useful body in that habitat. If what I have developed so far is acceptable, both credit and doubt must be equally bestowed on the polyp and medusa as the ancestral body form of the Cnidaria. The radial symmetry of the phylum could be an ancestral inheritance from the origins of the Metazoa, from evolution as planktonic organisms, or from sessility.

Embryology has contributed a great deal to our knowledge of phylogeny and some discussion of what evidence is available here seems well worthwhile. The turbellarian theory requires a flatworm as ancestral to the Cnidaria, and, interestingly, the free-living flatworms at least seem to have settled upon a very precise cleavage pattern known as spiral cleavage. This same cleavage pattern is typical not only of flatworms, but of nemerteans, annelids, mollusks, and certain additional minor groups. These seems to be little doubt that these great and successful groups, including the flatworms, represent a closely related series of phyla. Hence, one cannot but wonder why the Cnidaria, if they are derived from flatworms, show no signs of spiral cleavage in their embryology. Not only is there no spiral cleavage, but there is no single pattern of cleavage which is descriptive of the Cnidaria in general. This group instead shows a wide variety of cleavage patterns which suggests to me that they represent a very old group, in fact a group so old that cleavage patterns were still being experimented with as this group evolved. I do not believe that one can find a parallel anywhere in the animal kingdom to the one which the turbellarian theory asks us to accept. That is, it asks us to believe that the determinate spiral cleavage which runs through so many successful animal phyla was discarded along with the free-living mode of life, and in its place a whole new series of embryologies has been invented.

One additional and perhaps very significant feature of the embryology of the Cnidaria should be mentioned here. This is that the embryological axis is maintained as the adult axis by this phylum, as indeed it is by the Ctenophora. In all metazoans higher than these two groups, the animal–vegetal axis of the cleaving embryo is soon disguised as the organism assumes its adult form. Blastulae and more particularly gastrulae of many phyla have a simple radial symmetry around the animal–vegetal axis, but in flatworms and all higher groups this symmetry disappears and is replaced with bilateral symmetry. Our two hypotheses about the origins of the Cnidaria look upon these data in very different fashions. The medusa theory accepts the symmetry of the phylum as radial and the radiality is cited as evidence of the primitive nature of the group. The turbellarian theory assumes

the radiality to be secondary and cites the bilaterality of the Anthozoa as evidence. To my mind the maintenance of the embryological axes, as well as the fact that radial symmetry precedes bilateral symmetry in development, is evidence that the primitive symmetry of this phylum is in fact radial. The bilaterality of the Anthozoa will be discussed shortly.

The two theories before us contrast sharply in that one calls the Anthozoa the primitive class of the phylum while the other bestows this position on the Hydrozoa. In general I believe we can show that primitive groups are more variable and less fixed in body plan than are the less primitive or more highly evolved. As examples we could cite the Crustacea as more variable than insects, the polychaetes as more variable than oligochaetes or leeches, the gastropods as more variable than lamellibranchs or cephalopods, and the turbellarians as more variable than flukes or cestodes. If this principle is accepted I think we can also say the Hydrozoa are more variable than Anthozoa or Scyphozoa, and by this suggest that the Hydrozoa are the more primitive. I think one has only to look at the diversity shown among such hydrozoans as the tentacleless *Protohydra*, a hydromedusan, a siphonophore, a hydrocoral, and the pteromedusan *Tetraplatia* to see that this is greater than that exhibited by the other classes. In fact, the Anthozoa exhibit only two body forms, that of the alcyonarian and the zoantharian polyp. These two, while clearly separable, are none-the-less much more uniform between themselves than are the medusoid phases of the nine hydrozoan orders with medusae. We will add here, too, that the nematocysts of the Hydrozoa are more variable than in any other order, a matter we shall mention again. This seems further evidence of the primitive nature of this group. This evidence seems therefore to suggest that the Hydrozoa may be more primitive than the Anthozoa.

Although I do not believe any facts presented so far prove conclusively that the Hydrozoa are the ancestral group of the Cnidaria, we might in any event look at that class to see whether we might be able to make a decision as to whether the polyp or medusa is the primitive adult form there. Throughout the class we find that the medusa is the sexual adult and in most instances where the polyp is the possessor of gonads, we can show that these are borne on structures which are clearly medusoid in origin. Rees (1957) in what should become a classic article on evolution in capitate hydroids has concluded, as have many others, that the medusa is the original body form in this class and that the polyp is of secondary origin. This conclusion seems inescapable and as a corollary the life history of the trachyline medusae which involves no sessile polyps seems to be a logical example of what the primitive hydrozoan life history may have been like.

Earlier in this paper we noted the general agreement between modern theorists that the cnidarian ancestor was planuloid in body form. This planuloid organism must have been ciliated and most likely swept food into a more or less posterior mouth with the help of cilia just as do some ciliates. These planuloid organisms may have lived on the bottom or somewhere above it. We can well imagine a sensory tuft of cilia evolving as a useful anterior structure. Our planuloid may also have possessed structures similar to trichocysts, rhabdoids, or nematocysts. This particular feature seems to me a most critical point and needs careful consideration. Trichocysts as seen in various protozoans may be cnidotrichocysts, *with eversible structures like a nematocyst*, or typical trichocysts, of solid construction. These structures have several functions apparently, such as protection against predators, food capture, and attachment to the substrate. Rhabdoids, a turbellarian feature, have many varieties, *none nematocyst-like*, and are used for protection and temporary attachment. It is of interest that many of the apparently most primitive turbellaria do not possess rhabdoids.

The nematocysts of the Cnidaria come in many varieties, and they function, like trichocysts, in food capture, protection, and attachment to foreign objects. From this brief discussion of trichocysts, rhabdoids, and nematocysts we could well conclude from the modern distribution and function of these structures that our planuloid was more closely derived from the ciliates than from the Turbellaria. We can add here that nematocyst-like structures also occur in the cnidosporidians and the dinoflagellates. This reinforces our general point of the moment that the planuloid may have been closer to the Protozoa than the Platyhelminths.

How now might our planuloid have evolved? In the development of coelenterates the planula must grow tentacles, either as it becomes an actinula or medusa, or as it settles and attaches to become a polyp. Also, both the medusa and turbellarian theory suggest that the development of tentacles is intimately concerned in the evolution of the Cnidaria. That tentacles arise early in development and that they are characters of the Cnidaria is a matter of fact. Now, can we derive some conclusion about the early cnidarian from this information? Tentacles are used by cnidarians primarily as aids in the capture of active food organisms. We can now imagine our planuloid developing tentacles armed with intracellular nematocysts. As this little organism's arms contact small prey, the prey is stung and carried to the mouth. This newly tentacled animal fits our concept of the actinuloid, but where did it live? If it had been a creeping bottom dweller one wonders if tentacles spread out to the sides or trailing behind would have been practical. I would think these structures would have soon found themselves tangled with minute debris and difficult to work with for a creeping organism. It seems better, then, to imagine our actinuloid with a planktonic way of life, using its tentacles to capture other little plankters.

Another possibility must be discussed at this point. The turbellarian theory requires that sessility develop as a first step in the evolution of the Cnidaria. If we look at the many other sessile groups of animals we note that nearly all utilize ciliated surfaces in food gathering. This is a most successful way of life as is shown by the following list of sessile forms which feed this way: sponges, entoprocts, ectoprocts, most rotifers, phoronids, brachiopods, mollusks, sipunculids, echiuroids, polychaetes, ophiuroids, hemichordates, and urochordates. The only exceptions are the cnidarians, some ctenophores, the barnacles which capture their food with setous nets, and a few rotifers which have developed special traps. The Turbellaria, with their ciliated surfaces, would seem well preadapted to ciliary feeding if they became sessile. However, ciliary feeding is restricted among the Cnidaria to a few anemones and corals. Even in these forms, nematocysts capable of capturing prey are present, and these animals are seldom solely dependent on cilia for food gathering. The ciliary feeding here is best interpreted as a recent innovation. None of these facts seems to support a flatworm as an ancestral cnidarian. I find Hadzi's contention that a well organized flatworm gave rise to an anthozoan polyp unacceptable on this account alone, since by analogy the ancestral flatform should have evolved as a small particle feeder, not as a predator of the cnidarian type. The strength of our argument would seem to be that nowhere in the flatworms can we find an acceptable prenematocyst structure, but this can be reasonably presumed to have been present in our ancestral actinuloid. This suggests a very early, pre-flatworm stage, separating the two groups of organisms. Moreover, the development of tentacles by the cnidarian ancestor would seem best interpreted as related to a developed or developing predacious way of life in which nematocysts were playing an important role. These tentacles in turn would have handicapped a creeping organism and would seem to have been more effective

and meaningful to a free-swimming form rather than a sessile one.

Now to go a step further with our imaginative story of the evolution of the Cnidaria it would seem to be logical enough if our tentacled-actinuloid by simple and a slight change in form became a recognizable medusa. This would leave us with a hydrozoan medusa, probably of the general group of trachylines, as the ancestral cnidarian.

One would like some additional evidence for the scheme just presented and some indication of the primitive and basic nature of the actinula within the class Hydrozoa is available to us. Totton (1954) has pointed out that the actinula larva is widespread among the Hydrozoa, and Rees (1957) has noted that it is only among the more primitive families of the gymnoblastic hydroids that this larval form is found. From these facts plus our earlier conclusion that the medusa, not the polyp, is the primitive form of the Hydrozoa, we must conclude that the early Hydrozoa did indeed have an actinula larva. Thus, it does not seem unreasonable to imagine that the actinula was a free-floating planktonic organism and was ancestral to the primitive hydrozoan medusa. These conclusions do not tell us whether the Hydrozoa or the Anthozoa may better be considered the more primitive group, however, so let us turn our attention to that matter.

At the undated time at which cnidarians first made their appearance as a discrete phylogenetic entity, they must have had as their companions myriads of other *small* marine organisms. These other small organisms must have served as the food of our ancestral cnidarians, and it seems logical to invoke the use of nematocysts as intimately associated with food gathering. If this is accepted it now is logical to argue that the full grown adult cnidarians were themselves still quite small and that they most logically would have had simple guts. Complexly organized and divided guts such as are seen in the Scyphozoa or Anthozoa seem better interpreted as adaptations for handling large food, such as probably did not exist at the time of origin of the Cnidaria. I think too that the characteristic presence of nematocysts in the endodermal tissues of these two classes is a sign of their evolution in relation to large and active prey which, even after swallowing, still needed a coup de grâce. This line of thought leads, like others used earlier, to the Hydrozoa, with their simple guts free of nematocysts, as the primitive cnidarian.

Another matter relative to nematocysts can also be developed to support the medusa theory. Many Hydrozoa, although not the simplest groups such as the trachylines, possess a remarkable variety of nematocysts. In the class there occur all the major categories, rhopalonemes, desmonemes, haplonemes, and heteronemes whereas neither of the first two types occur in the Scyphozoa or Anthozoa. The rhopalonemes and desmonemes can be described functionally as being for adhesion and entwining respectively. These nematocysts are effective in holding minute, weakly-swimming prey, but they seem of doubtful utility in capturing large or active prey. On the other hand, the occurrence of only haplonemes and heteronemes, types specialized primarily for penetrating and poisoning prey, in the Anthozoa and Scyphozoa is evidence that these groups evolved later, along with larger and more active food organisms. We should note here too that nematocysts as independent effectors suggest an origin of these structures at a time before the evolution of nervous systems. Thus, the nematocyst might better stem from a protozoan ancestry than from a group as complex as the flatworms.

Another argument, related to feeding habits, can be developed to support our thesis. Loomis (1955) discovered that the omnipresent substance, glutathione, induced the feeding response in *Hydra*, even though no food substances were present. H. A. Schneiderman and H. W. Lenhoff (personal communication) have further shown that this response is widespread in

the Hydrozoa. They could not demonstrate its presence in scyphozoan scyphistomae or such anthozoans as sea anemones. Again in examining the feeding habits of the Hydrozoa we note that they typically feed upon very small metazoans and larvae. The contact of these small food items initiates an immediate nematocyst response, which when the organism is penetrated releases glutathione. This in turn apparently triggers the mouth-opening response. This is an exceedingly valuable bit of behavior since many organisms eaten by hydrozoans are such feeble swimmers and of such low specific gravity that there must be little in the way of mechanical stimuli related to their contact with the hydrozoan. The Anthozoa do not have this response system, and this I would correlate with their evolution as feeders upon larger, more active, and highly evolved metazoans. It must, of course, be admitted that many Scyphozoa and Anthozoa do feed on minute organisms and even detritus, but these forms possess either haplonemes or heteronemes or both; that is, they also possess nematocysts adapted to the capture of large and active prey. This evidence seems to argue that these organisms have only secondarily turned to small particle feeding and supports our contention that the Scyphozoa and Anthozoa evolved in the presence of larger food items than were available to the early Hydrozoa; that is, the Anthozoa presumably are more recent in origin than the Hydrozoa.

One feature of the coelenterates which might, if we could understand it completely, yield some important information is the position of the mouth. As the mouth develops in a planula it clearly is terminal in position, that is it occupies the center of the posterior end of the body as far as locomotion is concerned. The mouth of an adult cnidarian, polyp or medusa, also occupies a central position. Among the free-living flatworms the mouth occupies a ventral position and may be close to the posterior end of the animal, but as far as can be determined is never terminal. In the embryology of both the flatworms and cnidarians the blastopore develops at the vegetal pole. It remains there in the Cnidaria but among the flatworms it soon occupies a ventral position as a result of differential growth of the larva. Among all of the Cnidaria the mouth or blastopore develops and remains terminal. In view of its generally ventral position in the flatworms, it seems curious that there is no sign of this in such organisms as the creeping planulae of many anthozoans, had they descended from flatworms. I interpret the radial symmetry of the Cnidaria as embryos, as larvae, and as adults to be a truly primitive feature. It clearly is a feature of the embryo and of the planula and only as the planula of the Anthozoa develops its pharynx, siphonoglyph, and mesenteries do the signs of bilaterality occur. These last are adult features and are secondary. The terminal month of the Cnidaria then can be interpreted as a truly primitive feature. Only in the Cnidaria and Ctenophora is this true. Since terminal months seem to be lacking in small creeping animals such as ciliates and flatworms, I interpret the terminal mouth of the Cnidaria as having developed in the pelagic realm. This evidence favors the medusa theory.

A curious feature of the Cnidaria is that the planula attaches by its anterior end if it is to become a polyp. The polyp retains the same axes as the planula, but no "anterior" is identifiable in the attached stage. In all other sessile organisms, and the once sessile echinoderms, the mouth is accepted as an anterior structure. No matter what changes sessility brings on, this landmark seems to retain its anterior location. From these facts I conclude there are basic and profound differences between the Cnidaria and the remaining animal phyla. It is intriguing that, like the planula, the sponge amphiblastula attaches by its anterior end. Also intriguing is the posterior mouth of the Ctenophora. These facts reaffirm my contentions that

the medusa, a pelagic organism, is the primitive form of the Cnidaria.

The relationship of the anterior point of attachment and the posterior mouth in the Cnidaria is also of interest if we look to the flatworms for indications of its origin. Many types of adhesive organs occur in the Turbellaria, some of them at the anterior margin. These anterior structures seem to be used to hold food or in fact to capture it, while more posteriorly located attachment structures may be used to grip the substrate while the worm struggles with some food organism. The only example of a turbellarian flatworm which spends much of its life attached to the substrate which I can find is that of the Temnocephala. These animals attach by a posterior sucker, however, and have an anterior mouth. There may also be a small and anteriorly located adhesive area in certain temnocephalans, but the primary adhesion appears to be the result of posteriorly located structures. In the monogenetic trematodes too, the primary adhesive organ is posteriorly located, and in the rest of the Trematoda the primary adhesive organ is at least posterior to the mouth. The location of the primary attachment structures of the cestodes is not so clear, but if our interpretation of the attachment hooks in the procercoid larva of some pseudophyllidian tapeworms as posterior is correct, then their attachment, too, may at least primitively have been at the posterior end. Granted that there are devices for attachment at the anterior end of some flatworms, none-the-less this group today seems to have settled upon posteriorly located adhesive structures in those forms which spend any considerable portion of their lives as sedentary or attached organisms. From this, as from other arguments, I find it difficult to believe that some archaic flatworm attached at its anterior end and became a cnidarian.

Another discordant feature of the turbellarian theory concerns the fact that, while many sessile animals are hermaphroditic, the sessile Anthozoa usually are not. Quite typically such sessile groups as sponges, barnacles, tunicates, lamellibranchs, and bryozoans are hermaphroditic. Why, one wonders when there seem to be selective forces leading to an association of hermaphroditism and sessility, would the Anthozoa not also show this pattern? This seems all the more curious when we note that the Turbellaria are nearly universally hermaphroditic themselves. Thus we have the picture of a free-living hermaphroditic group giving rise to a dioecious sessile group. This is contradictory indeed. Also contradictory are the hermaphroditic but free-living ctenophores. While I cannot resolve all the contradictions here, I do feel that the dioecious but sessile Anthozoa seem unlikely descendents of hermaphroditic flatworms.

The turbellarian theory also asks us to accept other curious changes. For example as the evolution of the group progressed from flatworms to proper anthozoans the cellular mesenchyme gave way to the much less cellular mesoglea. Complex reproductive organs were replaced by simple epithelial gonads, and all signs of the protonephridial excretory system of the flatworms were lost. The only portion of the nervous system which was retained was the epithelial nerve net. Mesodermally derived muscles also disappeared and striking changes in embryology must have occurred; determinate spiral cleavage gave way to a curious assemblage of patterns of indeterminate cleavage. The derivation of the mesodermal layer largely from endoderm was replaced with a derivation nearly exclusively from ectoderm. While I readily recognize that sessility is accompanied by many changes as compared to related free-living forms, I do not see why the changes outlined above should have occurred. Valuable structures, even to a sessile organism, would need to have been lost and substitutes, no better than the original, had to be invented. This does not seem to me to be the way evolution operates, particularly as judged by other sessile groups. With sessility we see the loss of sensory and

locomotory structures and a nearly universal adoption of small particle or filter feeding as a way of life. We do not, however, see changes in such basic features as their embryology, origin of mesoderm, and organ systems. The degenerative changes suggested by the turbellarian theory are far greater than any parallel, other than the adoption of parasitism, demonstrates to us, and from this it seems impossible to accept the turbellarian theory.

A number of the difficulties I find in accepting the turbellarian theory are associated with differences in the mesoderm of cnidarians and flatworms. If now we examine the medusa theory we see what I believe is the primitive role of the third body layer as it is expressed in the Cnidaria. In planulae, actinulae, and small polyps, there is little need for a third layer. These organisms closely approximate the two-layered condition of a hypothetical gastraea and with their small size and few epithelio-muscular cells need little more than the cementing layer to hold them together. Their body form is maintained by cell turgor. What I am arguing for here is that two cell layers as seen in these larval cnidarians is a truly primitive condition. I find it entirely unacceptable to believe that the evolution of the Metazoa involved an evolution of three cell layers before two and that the Cnidaria have lost that third layer. In view of the tremendous success which animals with a readily recognized mesoderm have had, whether sessile or free-living, the idea that a phylum could afford effectively to discard the mesoderm is difficult to accept and indeed there seem to be no examples available. To go on beyond the primitive condition seen in planulae, the development of the medusoid form required the development of a very special structure, the mesoglea. Perhaps as an elaboration of the cementing layer, or perhaps as a new invention, the development of an elastic filler between the two body layers was necessary before the medusa could have evolved as a pulsating, swimming animal. In general function the mesoglea of the medusa increases buoyancy, gives form, provides a solid substance for the attachment of cells and is pliable and elastic. With increasing size, as seen in the Scyphozoa, more cells become involved in the development and maintenance of the massive mesoglea and even in the scyphozoan polyp there is a well developed mesoglea. The polyp of the Scyphozoa, however, foreshadowing the need for a large gut of its adult form, has become partly dependent on an aqueous skeleton. Water is driven into its coelenteron by cilia and the maintenance of an expanded state is dependent upon the maintenance of a slight pressure of water inside. The septation of the gut of the adult is also foreshadowed in the polyp here, and, as larval features, retractor muscles are developing along the four mesenteries. In the Anthozoa, as in the scyphozoan polyp, the mesoglea plays but a very minor role in the support of the body, but does provide much strength from its tough but pliable nature. Masses of fibers and scattered cells characterize this very tough mesoglea. Thus the mesoglea seems to have developed first in the Hydrozoa as an elastic skeleton against which muscles could operate and then been modified as a tough fibrous support for muscles in polyps. These suggestions give to the mesoglea the character of an early solution to increasing size and an acceptable functional role. They do not demand a change in role as would be necessitated if flatworm mesenchyme were the antecedent of mesoglea. To what extent mesoglea is a homologue of mesoderm is difficult to answer, but that mesoglea is a kind of mesoderm seems obvious.

I mentioned above the septation of the gut of the Scyphozoa. In all classes of the Cnidaria there are examples of guts which are more or less subdivided. Some trachyline medusae show pouched stomachs and the radial canals can be interpreted as a sort of division of the digestive system. These canals, however, are probably better thought of as devices to speed up the movement of nutritive materials to such marginal structures as tentacles. The

pouching of the gut is of course very obvious in the Scyphozoa and Anthozoa. The turbellarian theory requires these gut pouches to be interpreted as homologues of the pouches of turbellarian guts. If this is so we see some very interesting differences. The subdivisions of cnidarian guts occur by the ingrowth of mesenteries or septal sheets of tissue from the body wall, not as outgrowths of an endodermal sac as in the Turbellaria. These mesenteries also are radially distributed around the long axis of the polyp, not laterally as seen in the flatworms. Also, the pouches of the gut represent the great bulk of anthozoans and extend orally along the pharynx as well as to the very aboral extremity of the body. This is most unflatwormlike since the pouches should be well removed from the pharynx and should be distributed along the gut. The musculature which characterizes the faces of the mesenteries of anthozoan polyps has to be homologized with the muscles of the gut of the Turbellaria. It would indeed be remarkable if in the transition from worm to polyp, these intestinal muscles were transformed into the primary longitudinal muscles of the body. According to the turbellarian theory, the stomodaeum and bilaterality are the best preserved flatworm characters. The stomodaeum is necessary to a polyp as a muscular, food-handling structure and makes possible the separation of incoming and outgoing water currents. It is necessary if a siphonoglyph is to exist. The bilateral development of couples of mesenteries seems more readily referable to the organization of the anthozoan polyp around the functionally very crucial structure, the siphonoglyph, than to any ancestral reminiscence of a bilateral ancestor. In anthozoans having a strongly developed retractor on one face of the mesentery, this organization seems necessary since the opposite face is occupied by radial muscles and a mixture of the two sets would be a very unlikely organization. The bilaterality of the Anthozoa, therefore, is a superficial one, imposed on an ancestrally radial animal as a by-product of its own specialization in developing a highly efficient aqueous skeleton. There seems to be no anlage or homologue of a siphonoglyph or of the mesenteries of anthozoans in the Turbellaria and to point to these or the bilaterality of an anthozoan as a flatworm derivative is unacceptable. The presence of a stomodaeum in both groups seems in part referable to the solution of how to pass food on to an open gut, but solves for the cnidarian the problem of water transport too.

Before I close this paper and by way of summary, I think we might briefly note some points. My contention that the Hydrozoa are the most ancient of the Cnidaria and that the medusoid body form is primitive leads to the conclusion that the Cnidaria are a phylum of radial organisms. The radiality here is a by-product of evolution in the realm of open waters, not a by-product of sessility. Bilaterality as seen in the polyps of the Anthozoa must have evolved as a result of increasing size and the necessity to provide an aqueous skeleton against which the body musculature could operate. Thus the development of the siphonoglyph, the primary incurrent water structure, imposed on the ancestral radiality a superficial bilaterality. This bilaterality is, however, fundamentally different from bilaterality as seen in flatworms where dorso-ventral, left-right, and antero-posterior axes are present. Only the anterior-posterior axis is present in the Cnidaria with the interesting exception perhaps of the zoanthella larva of some zoanthideans. Here we find a recognizable ventral surface with long cilia. Some coral planulae may also show a similar differentiation. However, this phenomenon seems better referable to the creeping activities of these planulae than to their ancestry from any flatworm. The locomotory anterior ends of some planulae also show specialized sensory tufts of cilia similar perhaps to those found in flatworm and other larvae, but no such structures seem to occur in even the simplest adult flatworms. I believe we can better

conclude that the bilaterality suggested in some of the structures of planulae are purely larval inventions, not ancestral reminiscences.

We can also conclude from our earlier discussions that nematocysts may have played a crucial role in the differentiation of the Cnidaria from their forebears. These structures seem most readily derivable from protozoan structures such as cnidotrichocysts. Their occurrence as independent effectors strengthens this argument, and the specialization in the Hydrozoa of nematocysts and behavioral responses for the capture of minute prey argues for an early origin of this group.

The muscular system of cnidarians bears some intriguing similarities to parts of the musculature of turbellarians. Epithelio-muscular cells are known to exist in some of the lower Turbellaria, and Hyman (1951) has suggested that the subepidermal musculature of these organisms is homologous with the muscle cylinder of coelenterates. However, in the simplest turbellarian there is also a complex parenchymal (mesodermal) musculature, while the largest and most complex of the coelenterates, say a large sea anemone, possesses only epidermal musculature. Also, the gut of some turbellarians, if it has a musculature of its own, is sheathed in muscles of mesodermal origin, not with epithelio-muscular cells. If the Cnidaria had been derived from the Turbellaria, it seems curious that all of the mesodermal musculature would have been abandoned and that epithelio-muscular cells of endodermal origin would have been invented to replace the mesodermal muscles there. I would prefer instead to continue to believe that the cnidarian muscles are truly primitive, and that the mesodermal muscles of flatworms represent an evolutionary advance of that group over the Cnidaria.

The general absence of hermaphroditism in the phylum Cnidaria seems also to argue against the flatworms as ancestors and against the Anthozoa as ancestral even more so. Some Anthozoans are hermaphroditic, but this is a truly rare phenomenon in the class. Why more Anthozoa are not hermaphroditic in view of their sessile nature seems a riddle with no good answer.

The presence of two well organized tissue layers in the Hydrozoa can now be taken as a primitive feature, although the mesoglea certainly is indicative of a third tissue layer. The more abundant cells of the mesoglea of Scyphozoa and Anthozoa clearly mark these animals as triploblastic, but the pattern of derivation of this third layer from the endoderm has not yet set in. The nervous system of cnidarians must also be regarded as quite primitive. Its unpolarized and diffuse nature seem much more fitting as an early attempt at an integrated system rather than as a degraded system.

The embryology of the Cnidaria is a curious assemblage of different modes of cleavage and subsequent embryological activities. Essentially all of the phyla higher than the Cnidaria can be characterized by some specific embryological pattern. The cnidarian multivalence here, I think, must point to the origin of the group at a time so ancient that the Metazoa, in their newness, were still experimenting with varying modes of development. Whether this be a good interpretation or not, the fact that the Turbellaria and several higher and major groups of organisms have settled upon spiral cleavage as their way, and the absence of any sign of spiral cleavage in the Cnidaria, must weigh heavily against a flatworm ancestor for the Cnidaria.

Having reviewed the evidence available to me and having used what I hope are slightly new lines of reasoning, I have, for myself, answered the question posed in the introduction of this paper. That is, I conclude that the medusa was the body form of the ancestral cnidarian and that radiality is the primitive symmetry of the phylum. This conclusion accepts the medusa theory and rejects the turbellarian theory. As concomitants to my conclusions, I believe the flatworms as a phylum

must also stem from a "planuloid" but from a line well removed from the Radiata. The Ctenophora have been only lightly touched on in my discussion, but if we accept the recent evidence that this group may possess intrinsic nematocysts, along with other points noted, they must be placed close to the Cnidaria, if not reestablished as members of the Coelenterata. The Porifera remain safely ensconced on the phylogenetic tree, one branch below the Cnidaria. I must admit here that some of my arguments can be questioned by the simple device of turning them around, however, this is true only of *some* of them. The *balance of all the evidence* indicates that the Cnidaria occupy the position that the phylogenetic principle, *simple before complex*, dictates; that is, they are pre- not post-turbellarian in origin.

REFERENCES

CARTER, G. S. 1954. On Hadzi's interpretations of phylogeny. Syst. Zool., 4:163–167, 173.

HADZI, J. 1944. Turbellarijska teorija knidarijev (Turbellarien-Theorie der Knidarien). Slovenska Akad. Znanosti Umetnosti, Ljubljana, 238 pp. (not seen; note too several additional references by this author are cited by Hadzi in his 1953 article).

——— 1953. An attempt to reconstruct the system of animal classification. Syst. Zool., 2:145–154.

HYMAN, L. H. 1940. The Invertebrates. Vol. I. Protozoa through Ctenophora. McGraw-Hill Book Co., New York.

——— 1951. The Invertebrates. Vol. II. Platyhelminthes and Rhynchocoela. McGraw-Hill Book Co., New York.

——— 1959. The Invertebrates. Vol. V. Smaller coelomate groups. McGraw-Hill Book Co., New York.

JÄGERSTEN, G. 1955. On the early phylogeny of the Metazoa. The bilaterogastrea theory. Zool. Bidrag, 30:321–354.

LOOMIS, W. F. 1955. Glutathione control of the specific feeding reactions of hydra. Ann. New York Acad. Sci., 62:209–228.

MARCUS, E. 1958. On the evolution of the animal phyla. Quart. Rev. Biol., 33:24–58.

REES, W. 1857. Evolutionary trends in the classification of capitate hydroids and medusae. Bull. Brit. Mus. (Natural History), Zool., 4:1–60.

TOTTON, A. 1954. Siphonophora of the Indian Ocean. Discovery Reports, 27:1–162.

CADET HAND is assistant professor of zoology in the University of California at Berkeley. He specializes in the life history and systematics of hydrozoan and actiniarian cnidarians.

The Functions and Limitations of Classification

R. E. BLACKWELDER

IN SPEAKING of classification of invertebrates in general, I speak not as an authority in any group but as a person who has been interested in the classifications worked out by other people *and* in the justifications they give for their conclusions. In following out this interest I have seen some excellent work on classification of obscure groups. I have seen groups in which almost no classification is being attempted, only descriptive taxonomy, and I have also seen some very poor classification.

A few years ago my course in such a lecture as this would have been clear. Pick out the most important failures of classification, especially the faulty premises, and try to illuminate them. Today the situation has changed enough so that I can scarcely proceed in that way, and you will soon see that our chairman is the person largely responsible for this.

It has been evident for a long time that classification of animals has been plagued by a series of hypotheses that attained such a firm hold that no one even dared to speak about the possibility that they might be faulty. I am not thinking of the philosophical basis of classification, although false premises also exist in this field, but rather about specific major features of animal classification.

The too obvious simplicity of symmetry relationships, the false importance placed on mode of coelom formation, the assumed comparableness of metagenesis in various groups, the idea that phylogenetic speculations form an important basis for classification, the supposed chordate nature of the Hemichordata: these and many other ideas have been ripe for criticism.

Some time ago I wrote a review of a series of books that makes a very large contribution to many of these questions. Strangely, it is not apparent in the title or plan of the series that such things will be discussed, and many people know the magnificent set of the INVERTEBRATES by L. H. Hyman only as a masterful compilation and synthesis of the knowledge of the smaller invertebrate groups. No review was necessary to record this aspect, but I was interested in quite a different feature of these books. I refer to the forthright, iconoclastic, and generally sound discussions of particular features of the generally accepted classification of animals and also of such more general aspects of zoology as recapitulation, polymorphism, germ layers and their formation, the origin of metamerism, and so on.

I do not mean to say that I think these books have settled all the problems of invertebrate classification, as they have dealt with only certain ones of them, but the manner of attack has broken the ice and opened the way for us all to reconsider the very basis of our beliefs. And I do mean beliefs, because all of us accept things which we cannot justify and claim there is basis for ideas for which we can produce no real basis. This is the nature of the strange organ we call the human mind.

I should add that I also do not intend to imply that I agree with every one of Hyman's conclusions. But I do feel that when I disagree, I had better be sure of my facts, lest she confound me in my own errors.

For about two decades systematics has been under pressure to accept certain ideas as gospel and unchallengeable. The pressure has been so great that few systematists have spoken out against the dogmas. Now that we are encouraged to reexamine and speak out against the entrenched errors of classification, perhaps we will also have the courage to reexamine and speak out against the equally dogmatic errors that are being imposed upon us by overzealous vertebrate specialists under the guise of a new modern approach to systematics.

Classifying

There has been much written about classification in the last two decades that has been based on certain beliefs that are unproved but were tacitly assumed. I have seen the statement that since we all know that all organisms are either plant or animal, it is foolish to discuss the possibility of whether there might be three or more kingdoms. The only way we can "know" this is if we tell ourselves that it is true. Nature has not given us any such piece of information, for Nature does not recognize any distinction even between plants and animals. To argue that because Linnaeus separated the living things known to him into two kingdoms proves that there actually are only two, is the most specious sort of argument, not worth the time to deny it.

However, in the same unsound type of argument we hear it said that classifications MUST be based on phylogeny or at least reflect phylogeny. Who says it must? What law of the universe makes this so? It is possible that we might agree to a definition of classification that would in-

volve phylogeny, but so far we do not have complete agreement, merely the dogmatic assertion that anyone who denies the statement is a crank and not to be taken seriously. The disagreement is much stronger than generally realized, on this and many other subjects, and it seems evident to me that systematics will progress much more soundly after these disagreements have been worked out objectively, rather than by repetition of catch phrases that are appealing but may be misleading.

Classification is many things to different people. This is obvious in the definitions given in our textbooks. A variety of things are cited as the basis of classification, and a variety of other things are cited as the units of classification. There is a variety of definitions of what a natural classification is, with quite unusual agreement that such a "natural" classification is desirable. There is a variety of meaning for key words in classification, such as category and species.

Classification is one of the oldest methods of thoughts employed by man. The people who study the processes of thinking tell us that classification is involved in judgment, memory, problem-solving, inventive thinking, esthetics, perception, and concept formation. Is there anything else that the mind can do?

Biologists, and perhaps all scientists, have a tendency to shun philosophy and metaphysics, perhaps merely because they do not understand them, and along with these they are likely to neglect formal logic and related subjects. As a result some biologists have claimed that biological classification is different in kind from logical classification and must be viewed in a different light. There seems to be no basis whatsoever for such a claim. It is very likely true that biological classification is much more involved than most others; there are more things to be classified and more possible ways in which they may be classified. But greater complexity does not change the nature of the process, even though it may introduce some new problems.

Classifications may be complex but the process of classifying is essentially simple. It is not the recognition of something that exists in nature, for nature is not classified. It is the invention by man of ways in which events and things can be grouped, for the sole purpose of increasing his ability to deal with the events and things. Man has discriminative capacities far beyond his ability to remember the details, and he escapes from this dilemma only by classifying his concepts. He then thinks of the events and objects as members of a finite number of classes rather than as individuals, *ad infinitum*.

This is exactly what biologists do in classifying the objects we call animals. Every one of the biologists who are also familiar with logic and the methods of epistemology acknowledges that the process is the same in biology as elsewhere, has the same conceptual basis, and in fact cannot be different because this is the nature of man's mind.

If there is any doubt that this is true, the doubter should try to recall any important advance in the classification of organisms that was made by any other means than by grouping the objects or concepts and arranging them in a hierarchy or system of categories. I doubt if a good example can be found.

There is much apparent difference of opinion as to what it is that we are classifying. Some writers claim that the species is the basic unit of classification. There is no question that species can be classified. Epistemologists tell us that one can classify anything that enters his mind. This means one can classify any concepts, because concepts are what the mind sees when it receives sense impressions or when the imagination is at work. These concepts may represent either objects which have been seen (or imagined) or the concepts representing many objects or ideas combined. In my mind there is a concept representing this object—this

table—and there is another concept representing the composite idea of table—all tables at once.

"A Species," a particular species, species x, is one of these composite concepts. It is made up of the images of all the individuals that have been seen. We classify species in every biological classification.

It is equally possible to classify objects. In this case the objects are individuals. We do this constantly when we sort out specimens and say that these belong to Species A.

Now, if we leave out classification of hypothetical things, imaginary ones, we can recognize one limitation to classification—we can classify only what is before us, either actually or figuratively. When a man says he is classifying species, we can ask him, "Whence came these things you call species?" He can reply either, "I sorted these specimens into groups which I consider to be species" or he can say "I am classifying the species described by previous workers." In each case he admits that there first were individuals that had to be classified into species. A man *can* classify species, but only if someone before him has already classified individuals to produce the species concepts.

It has become popular recently to contend that the species exist in nature and can thus be classified as objects. This may be true, but it does not alter the situation one whit, because we do not actually classify the species at all, in the sense of sorting objects into piles, because we have never held a species in our hand. We merely hold a conception of it in our head, and we put this conception into words or pictures as best we can. Whether or not the species exists is beside the point. Species, like objects, can be classified only when they are conceptionally before us, but unlike objects, species are concepts only after one or more individual has been seen and classified as belonging to that species.

This misconception of what is the real basis of biological classification may have arisen through a distinction that was at one time made between taxonomy and classification. The taxonomy was held to include all matters dealing with individuals and the grouping of them into species. Classification then took over and dealt with the groupings of species into more inclusive groups. There is no justification for such a distinction. Taxonomy may be principally description and identification of individuals, but classification involves the individuals as well as all the groupings of them.

The Animal Kingdom

I think there can be no question that the classification of invertebrates which we now have is a very good one, considering that it must order the knowledge we have of nearly a million kinds of animals. In this connection we may wonder at recent statements about the "confusion" in zoological classification, about the inability of systematists to agree on some points, and about the so-called failure of taxonomy to achieve its goal. It is apparent that these ideas usually come from students of vertebrates, and it may be useful at this point to have a look at the difference in the problems facing the classifier of vertebrates and the classifier of invertebrates.

Figure 1 is a diagram adapted from one prepared by S. W. Muller of Stanford University. The area of the full circle represents all the known kinds of animals. One quadrant is marked off and divided into five roughly equal parts. If we divide the circle into vertebrates and non-vertebrates, one of the fifths of this quarter would be the vertebrates and the rest of the circle would be non-vertebrates. Nearly 95 percent of all kinds of animals are non-vertebrates. Must we conclude from this that ideas drawn solely from knowledge of vertebrates justifies sweeping statements about all animals? Does the state of taxonomy of part of these vertebrates justify the statement, recently published, that this work of distinguishing

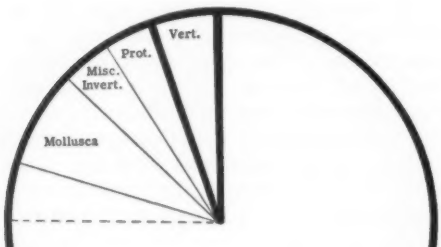

FIG. 1

the types or forms of organisms has been completed?

We all know that there is no such thing as a "group" of animals composing the Invertebrata. The Vertebrata is a single group characterized by certain positive characteristics, but the invertebrates are merely all the rest of the animals, a dozen or a score of widely distinct groups, usually with little in common except the features that are also shared with vertebrates. This assemblage of groups contains both extremely small groups and extremely large ones, whether we are thinking of phyla or classes. It even contains one family that is about the same size as the entire Vertebrata.

Among these groups there is one that is more isolated than most. This is the Protozoa, which in size would roughly be a second fifth of this one quadrant. As this group is customarily included with other non-vertebrates in elementary courses, I have dealt with them in both beginning and advanced courses on invertebrates. I was therefore surprised to find that in both courses the Protozoa are a disturbing factor. They do not properly fit into many of our concepts from multicellular animals and require separate treatment if they are not to obscure two pictures, that of their own nature and activities and that of the nature and activities of the Metazoa.

The remaining 90 percent on this diagram are the multicellular invertebrates in the broad sense. One of the three remaining parts of the quadrant shows roughly the size of the Mollusca, the second largest phylum of invertebrates. The second would represent the remaining groups of invertebrates together except for the giant group Arthropoda, which is represented by the remaining fifth plus the other three quadrants. The three quadrants together show the size of the Insecta, whereas the fifth indicates the known non-insect arthropods.

I think that this diagram should be required study for any vertebrate specialist tempted to generalize about animals in general. This should lead to a reduction in the number of statements about animals that are really applicable to only 5 percent or less of the animal kingdom.

What are some of these statements? For one, the idea that our taxonomic species must be based upon the ability to interbreed and produce fertile offspring. This sounds like a reasonable criterion, but in practice it is utterly unusable on a practical level in all but a mere handful of groups. The variety of sexual developments in the various invertebrate groups come close to making such a distinction meaningless. For another, because of the small number of species in each class of vertebrates, the idea has spread that a sharply limited number of categories in the classification hierarchy can be considered standard and any others as merely excess baggage. Mammalogists consider it necessary to use 14 categories to show the arrangement of some 5,000 species in their class. Do they expect malacologists to be able to arrange satisfactorily 80,000 species of Gastropoda with the same number of categories? What of entomologists, with at least 700,000 species?

In my opinion, the classification of invertebrates, incomplete as it is, has already been amazingly successful in bring-

ing much order to a veritable infinity of facts about the multitudes of very different invertebrates.

Successes of Classification

The major success of taxonomy is this one just referred to—the building over two centuries of a classification of animals that has served its major purpose admirably, has proven to be almost infinitely flexible, and has contributed far more to other branches of biology than they usually realize or acknowledge.

No taxonomist in his right mind would contend that our classifications are perfect, or that the work is finished or even nearly finished. But they *have* reached a point at which we seldom find them completely inadequate. In speaking of the new forms that are discovered daily in the great museums and elsewhere, Calman remarked that, "Seldom, very seldom indeed, do we come across a species for which there is not a place waiting in the accepted classification." We know that advances are being made continuously, through the incorporation of new data, but the key word here is "incorporation." Very seldom does a classification have to be really done over from the beginning. Rearrangement or redefinition seldom amounts to a fundamental change, because it is the groups which are of most importance, and they nearly always survive the rearrangement.

This idea of the importance of the groups rather than their arrangement is worth looking into further.

It has been said that great confusion reigns in the segregation of groups at the higher levels of the categorical system, among the classes and phyla. Mayr in 1942 wrote that "There is extremely little disagreement in well-worked taxonomic groups as to the limit of the species (but) such agreement is utterly lacking as regards the higher categories."

Do you agree that there is extremely little agreement as to what are Mollusca? or Echinodermata? or centipedes? or rotifers? In well over 99 percent of all animals, living or fossil, there is no doubt whatever of the order, class, or phylum. In fact there is so little disagreement as to the contents of most groups that we can reasonably say that the problems of classification today are largely the disposition of lesser known or anomalous groups. In both of these, the great need is for more facts on which to base conclusions.

Just what are these "groups" of which we speak so glibly. At the lowest level each of them is the series of *individuals* possessing certain features in common. At all higher levels each is the series of *groups* possessing features in common. The essence of classification is thus the grouping of like objects *or* groups.

A recent zoology textbook tells us that taxonomy emphasizes the differences between organisms. This is true only if we are looking at it *after* the work of classifying is done. At *that* time the very grouping of likes serves to highlight the fact that the groups are different. Nevertheless, real classification always employs similarities, and the differences appear merely as a by-product.

Even in the invertebrates the grouping of like things into groups on various levels has already been carried a long way. All but a very small number of animals can be placed with similar animals in one of the phyla. Even if we consider extinct forms, there are still relatively few that cannot be placed in a class within the phylum, where they fit into the pattern of the other members of the class. And no matter what level we consider, there are few animals among the known hundreds of thousands that cannot be placed with similar organisms in groups that have a certain unity. Where we *do* find difficulty is in determining whether any particular group belongs at the level of order or subclass or superfamily. But about the groups themselves there is little disagreement and no obvious confusion.

The places in invertebrate classification where the most disagreement occurs

would probably itself be the basis of disagreement. It seems to me that one place is in the Crustacea, where anything like a final classification seems yet to be out of reach. This appears to be a group of immense variety and relatively slight difference, in which groups made on one basis cut across groups made on another basis. I suspect that a solution awaits more complete summary and analysis of groupings.

Another place of relatively great disagreement is the Arachnida, in the broad sense. This group has for a long time been an orphan, neglected by invertebrate specialists and inadequately treated by entomologists. But this is not the only cause of difficulties in this group. Too many current workers seem to refuse to employ the sound analyses that have been produced. They prefer "convenient" arrangements to sound ones. The first president of the Society of Systematic Zoology, Alexander Petrunkevitch, has done some of the very good analytical classification—work which has never been equalled in the Arachnida and which can be neglected only to the detriment of all later work.

A third place that has seemed "soft" to me, is the series of groups often placed between the Echinodermata and the Vertebrata. I use the latter name intentionally here, because I wish to include in the "soft" area the so-called non-vertebrate chordates. In this case, Hyman has recently helped much to clear the air, with forthright commentaries on some long-standing errors or inadequacies.

These three cases illustrate groups which may be thought to be inadequately classified in different senses of that expression. But these do not illustrate the few cases mentioned before in which the animals cannot be placed in groups. There is quite a long list of the latter, but many of them are known only from fossils. They are unplaced because of a variety of reasons. First, some extinct animals are known only from preserved hard parts. They cannot readily be placed in a classification based principally on the organs of the living animals. Among these we may cite the conodonts, the graptolites, the conularids, the stromatoporoids, and the eurypterids. Second, there are some that are not placed in groups because they simply differ so much from all others that they stand alone. Here we may place the Mesozoa, the Pogonophora, the Onychophora, and the Chaetognatha.

Third, there are some that have been seen only a few times and the recorded information is not sufficient to place them in the classification. One of the best examples of this is *Salinella*, in which only part of the life cycle is known and examples are not available for further study.

It is possible to make quite a list of these "difficult" groups, according to your own ideas about difficulty, but they form altogether an insignificant number among the known organisms. They do not at all justify the statement that our classification is confused and entirely inadequate.

At the same time it is often these unusual groups that are of the most interest and importance in zoological speculation. Specialists on most of these groups are making headway in solving their problems, and that is all we can expect of them.

Failures of Classification

Failures of classification may be either the failure of our systems to produce the results we anticipated, *or* the failure of taxonomists to make adequate use of classification.

There are some people who believe that our system of classification is inadequate because it cannot do all the things that they have demanded of it. It cannot show all the sorts of ecological-preference groups within populations. It cannot show the phylogeny of the species. It cannot show the hybrids, polyploids, gradients, and so on which we may wish to record. The reply to such criticism is obvious: the classification was not designed to show these things. It is hardly a failure of a radio set to be unable to produce

visual images—it was designed to produce only auditory reactions. So our classifications are suited to record information about individuals and groups of individuals—not to record genetic data, ecological data, or phylogeny.

The major failure in the *use* of classification is the failure to note and understand the fact that the purposes may vary.

The general purpose of all classification of ideas is to bring order to a mass of data too great to be fully understood separately. But every classification will by its very nature serve only the purpose for which it was designed. A classification of books by subject will not be usable in the same way as one by author or date. A classification of animals based on structure will not be useful for the same purposes as one constructed on ecology or geography. A classification based on males may be of no use in dealing with females, and so on.

There are many biologists who insist that biological classification must be natural, and that "natural" means that the members of each group had a common ancestor, or, that the arrangement reflects or is based on phylogeny. It is usually not clear what is expected of such a phylogenetic classification. It is evidently not to *show* phylogeny, because it is usually *based on* phylogeny. If one wishes the classification to reflect the phylogeny, then it is proper to base it on data that show the phylogeny, if such are available. This system could then be used in correlating organisms of varying degrees of relationships—varying distances back to a common ancestor. If this yielded new data or useful speculations, it would be justifiable as increase in knowledge.

In nearly every case of classification of animals in actual practice, the primary purpose, usually implicit, is to enable zoologists to identify and keep track of numerous kinds and infer data from one to the other. After we have dissected and studied several species of one genus, we believe it unnecessary to study in equal detail all the others, because they will be the same. The assignment of fossils to groups known from living species always involves such assumption. When we place a new species in an old genus, we do not say that we know it agrees in every respect with all the other species but that we have found that it agrees in enough features to justify our believing that it does agree in other pertinent features also.

This inference of unknowns from knowns in the classification is the real purpose of most classification. It is the reason why we want the known data ordered in what we call a classification.

Failures of Taxonomists

Some zoologists evidently believe that it is a major fault of taxonomy not to have completed a final classification of all animals that shows all the actual relationships between groups. There are at least three false suppositions here: first, that all animals are now available for study; second, that all classification is something objective which can in principle be fixed and final; third, that taxonomists have accepted in practice the goal of producing phylogenetic classifications. These three things will not seem equally erroneous to many of you, and yet the recent history of taxonomy shows that none of them have been actually accepted by taxonomists in classifying animals.

One of the things that taxonomists can properly be charged with is failure to understand the nature of the classification process sufficiently to avoid pitfalls. For example, much time has been spent, and I think wasted, on arguments over whether, for example, the spider group should be called an order, a class, or a subclass.

There is no particular difference of opinion about what animals are to be included in the group, and this is the important fact. There is no objective way for us ever to determine the category in which the group should be placed, so there is

little to be gained by arguing any one view.

This is the problem of the categorizing of groups. In the acute form it is the problem of preventing the elevation of groups to higher and higher levels without reference to conditions in other groups. The problem is *possible* because there is no objective way to determine the proper level in the hierarchy, and is made *likely* by the specialization of taxonomists who become engrossed in the structure of one group, and lose sight of the others.

Thus, we are confronted with a classification of a small group of animals—the fishes—three classes if you wish but only 40,000 species, that is now classified into more than 600 families. In some other parts of the animal kingdom there are single families that contain this many species. This discrepancy is not surprising—not cause to say something is wrong—for nature does not submit to patterns.

But in the fishes the cause for the recent increase is obvious. Most previous families have now been made orders; each section of what might once have been subfamilies or lesser groups have now been made families. There seems to be no question that these families are actually out of accord with families elsewhere; they are principally the result of a continuing tendency to elevate groups into higher categories. Such wholesale elevation is not the work of taxonomists who understand the nature of classification; because it does not solve the problem encountered in any advantageous way and it definitely creates new problems of substantial nature.

We must remember that our classifications are not open-ended; they are tightly closed. At one end we have the individuals, or, if you prefer to classify species that result from someone else's classification of individuals, then we have species. In classification, these are indivisible by definition. At the other end we have phyla or kingdoms. Our problem is to produce system or orderly arrangements of all known animals between these two limits. When we feel cramped for levels at the lower end of the range and solve the problem by elevating the groups to higher levels to make more levels available near the bottom, we merely make trouble at the top where there have also never been enough levels to show the obvious groupings that we want to record.

There is not even a theoretical possibility of showing all the existing relationships in any practical system of categories, so we must recognize that only the most obvious and useful groupings can be shown formally. There is no way for us to assure that groups at one level will be of similar value in different phyla, because the animals are simply too different. But we can try to use words like class and order in a way that will not add to the difficulties of classifying a million kinds of animals.

Another major failure of taxonomists is the strong tendency to base our concepts on the study of only a small part of the animal kingdom. Most discussions of theoretical considerations are based on experience with vertebrates alone, as if they were typical. Most generalizations in our textbooks hold for vertebrates but fail miserably when invertebrates as a whole are considered.

Thus, the rule that animal growth is primarily a matter of increase in number of cells breaks down among invertebrates. The concept of sexuality breaks down repeatedly and in several ways. The very distinction between animals and plants breaks down. The idea that we can trace in the fossil record the *origin* of major groups from other groups, showing that all animals arose from a single kind, breaks down completely because most major groups of invertebrates appear well developed at the beginning of the fossil record. The distinction between embryo, juvenile, and adult breaks down. The once-popular theory of recapitulation breaks down repeatedly or is at least completely eclipsed. The nature of species in lower groups simply cannot be under-

stood in terms of ideas based on vertebrate species alone. Cleavage of the fertilized egg, gastrulation, and cell determination are not to be understood from vertebrates alone. There is no end to this list.

The wonderful variety of nature simply cannot be taught or understood from the study of one group of animals, particularly not from the most homogeneous of the large phyla. It has been said that all animals exhibit the same basic features and the same functions. It *is* true that all animals respire, in the cellular sense, but they do not all use the same or even comparable means to do it. Do the vertebrates tell us of respiration by tracheal tubes or a respiratory tree? It *is* true that in all animals new individuals arise from parts more or less separated from pre-existing individuals, but do the reproductive processes of vertebrates tell us about protandry, hologony, polyembryony, hermaphroditism, all the forms of sporogony and schizogony, or obligate parthenogenesis? Will the vertebrates teach us about reproduction by budding, strobilation, pedal laceration, or autotomy? And how much can we learn from vertebrates about colony formation, about parasitism, about polymorphism, mimicry, or ecdysis?

In the constant effort to simplify biology for teaching purposes we have submerged the evidence that variety is the most obvious feature of the animal kingdom. In demonstrating that this variety can be classified and thus brought within mental grasp we have too often allowed our own nature as a vertebrate to obscure the extent of variety among invertebrates.

This seems to be partly the fault of students of invertebrates, who are too busy accumulating data to give much time to generalization or even to expounding the endless variety they have uncovered. Some students of higher vertebrates, apparently believing that the work of classification is finished, have dominated the theoretical and generalizing aspects, impressing their horizons (limited to one small phylum) on the statements that greet the beginning student. All zoology suffers from this, because any generalization is attractive to the learning mind, and any simplification is welcomed by the student who is overwhelmed by the endless mass of data. Once implanted in the mind, the generalization becomes dogma, an idea that is believed but not proved. It is usually there to stay, regardless of whether or not it gives a sound understanding. Science has found it impossible to use religious dogma, and must be equally ready to reject dogma originating in science. No ideas are so perfect that science can afford to accept them without constant re-examination.

There seems to be a great deal of similarity between the methods of classification used by different taxonomists, but there is no agreement at all on the generalizations we should make about the process and about our results. This is surely the major limitation on classification—that we can never make the best use of something that is misconstrued, misused, and maligned. Worst of all, it is too often being mistaught, so that understanding of the real nature and usefulness of classification is not being given to our younger zoologists.

But classification *is* essential to biology, and I have no doubt it will survive all of us.

RICHARD E. BLACKWELDER, Department of Zoology, Southern Illinois University, Carbondale, Illinois, is a taxonomic specialist in insects, particularly interested in classification and nomenclature.

Ancestors, Embryos, and Symmetry

MICHAEL J. GREENBERG

THE FOUR lowest multicellular phyla —Porifera, Cnidaria, Ctenophora, and Platyhelminthes—have in common that they are all, topologically speaking, double-walled sacks. Beyond this, of course, the great mass of data indicates that there is a singular lack of relationship among them. Accordingly, they are classified in separate phyla.

Most students agree that these lower animals have their immediate origin in the Protozoa. This is reasonable. The Protozoa are a large and diverse group which have not only frequently produced colonial forms and multinucleate forms but have also repeatedly given rise to other sorts of multicellular organisms.

There is no fossil record chronicling the derivation of Metazoa from Protozoa. Consequently, aside from a high probability that such an event occurred, the data indicating the non-relationship of sponges, coelenterates, and flatworms are unpolarized with regard to time. That is, so far as anyone knows or ever will know, the four simplest phyla could as well have descended simultaneously from different unicellular ancestors. It is common, however, for phylogeneticists to polarize the data artificially by making axiomatic assumptions defining primitivity. Once this is done, two structures or mechanisms which are merely different become temporally oriented as well. A logical phylogenetic story thus emerges with imagination helping over the inevitable rough spots. The probability of error must be large when logic is substituted for known time relationships. At low levels of organization, such as occur in the phyla mentioned above, not only time but also structural relationships are uncertain. Under such circumstances the chances of error in the phylogenetic picture increase (Bader, 1958).

In dealing with the relationships of the lower multicellular animals, as well as with their alleged ancestors, two principles are germane:

First, there was considerably more evolution of structure and physiological mechanism before the advent of the Protozoa than took place in the time which elapsed between the Protozoa and the appearance of the first Metazoa. Consequently, much of the biology of the simple multicellular animals can often best be explained in terms of interactions at the cellular level. Certainly we cannot expect more in the way of mechanism from the ancestors we choose to postulate than we can from their present-day descendants. This principle has been overlooked, for example, in Jägersten's (1955) clever derivation of the sponges from his bilaterogastraea. It is postulated that the sponge osculum develops with time from the anus of the bilaterogastraea, while the ostia develop from this creature's mouth. While the anus moves up one side of the presumptive sponge and remains intact, the mouth moves up the opposite side and breaks into the thousands of ostia with which sponges are equipped. This is simply too sophisticated a phylogeny for animals which, even today, have all they can do merely to keep themselves together.

The second idea, referred to above, really follows as a result of the first. It is that homology, as a phylogenetic argument, often fails when one is considering such low levels of organization as exist in the sponges, coelenterates, and flatworms (see especially Grimstone, 1959). The effectiveness of homologous struc-

tures as proof of common ancestry increases: 1) as the number of other possible analogous structures becomes large, 2) as the number of other animals possessing the structure becomes relatively small, 3) as the number of other similarities between these animals becomes large, and 4) as the complexity of the structure increases. When the level of organization of a biological system decreases, the number of analogies decreases while the number of otherwise unlike animals having similar, relatively simple, structures increases. As Grimstone (1959) points out, the cilium is illustrative. There is very likely only one way of making a cilium: the familiar "nine-plus-two" pattern. Most animals (if one excludes arthropods) have cilia and most animals which have cilia have nothing else in common. Another obvious example involves the body form of the phylum Cnidaria. The medusa, for example, is duplicated by the cystoflagellates *Craspedotella pileolus* and *Leptodiscus medusoides*. The Ctenophora also mimic this morphology. Both medusaform and ctenoform body patterns are suggested by Weill's (1946) "gymnostome" *Ctenoctophrys chattoni*. The shape of these diverse animals probably has arisen independently. In each instance the body form, a simple one, is the result of the evolutionary stimulus of the environment acting on masses of protoplasm, with the same genetically produced polarity, inhabiting approximately the same niche. Examination, in this light, of Hanson's (1958) view suggesting a common ancestry for Acoela and gymnostomes on the basis of similar body form and habit reveals that such an argument is probably invalid (Grimstone, 1959).

Nematocyst-like structures, while a less obvious example, may turn out to be illustrative of the failure of homology at low organizational levels. As is well known these structures are not only to be found in the Cnidaria. Apparently, they are also to be found endogenously in one species of ctenophore. Similar objects are seen in ciliates, dinoflagellates, and cnidosporidians. As Hanson (1958) points out, the sagittocysts of Acoela are reminiscent of nematocysts. One interpretation of such a distribution of these organelles is that Cnidaria and Ctenophora have a common ancestor which, in turn, is fairly closely related to the Protozoa (Hand, 1959). However, another interpretation might be that, aside from possessing these nematocyst-like structures, the organisms have nothing else in common which suggests a close relationship. It might then be more logical to reason that, given the proper fibrillar proteins and time, a system would evolve with an inherent "designing tendency" resulting in nematocyst-like objects (Picken, 1953, 1957). One would then expect such objects to arise often in diverse forms. Such a view is supported, firstly, by the crystalline behavior of the tube and its barbs (Picken, 1953, 1957). Secondly, it is urged by the mode of origin of these objects simply as protein inclusions in the Golgi complex of interstitial cells (Slautterback and Fawcett, 1959).

Making use of the two ideas—low organizational level and resulting failure of homology—let us consider the phylogenetic significance of planuloid ancestors, cleavage patterns, and symmetry.

Planuloid Ancestors

The cnidarian gastrula is often a stereogastrula—the planula. It is a ciliated, elongated, polarized organism with a columnar ectoderm enclosing a mass of endoderm. It is considerably differentiated (Hyman, 1940). The gastrula of many lower turbellarians is likewise a stereogastrula. This correlation, together with symmetry considerations to be discussed presently, has resulted in the postulation of various planuloid or gastruloid ancestors for the Metazoa (e.g., Hyman, 1940; Hand, 1959; Jägersten, 1955). While the arguments put forward in favor of such ancestors are cogent, the various lines of evidence mentioned below suggest that,

whether or not they existed, no phylogenetic significance can logically be placed either on the ancestors or on the planuloid-type larvae.

Firstly, most students will agree that the Porifera are related neither to the Cnidaria nor to the Platyhelminthes. This unique position is based on the presence of collar cells, which are found only in sponges and choanoflagellates, and on the unique method by which the germ layers and polarity of the adult are established. Nevertheless, perfectly good planuloid larvae occur in the sponges (e.g., *Clathrina*) in spite of the fact that they have no common ancestor with the so-called Eumetazoa. The gemmules of marine sponges, a mechanism of asexual reproduction, develop into flagellated stereogastruloids resembling those which arise from cleaved eggs. It is usually stated that, with the exception of one genus (*Gastrodes*), there are no planula larvae in the Ctenophora. However, a planuloid *embryo* is formed complete with stomodaeum and comb rows. It simply is not released until the cydippid morphology has emerged.

Secondly, planuloid forms occur in the Cnidaria, not only in ontogeny, but also in the course of asexual reproduction. The scyphystomae of *Chrysaora,* for example, after eating heavily until August, become moribund and autotomize their tentacles. These develop into polyps (see Berrill, 1949). In the same animal, cysts form under the pedal disc of the scyphystoma. Such cysts yield, under the proper conditions, ciliated larvae which are essentially planulae. In *Cassiopeia* ciliated buds which develop as planulae are constricted off the upper part of the stalk of the polyp (Hyman, 1940).

Thirdly and conversely, there are situations in which, on the basis of common ancestry, one would expect to find planuloid larvae but there are none. Primitive *Haliclystus,* for example, has no ciliated larva; creeping forms, similar to the frustules of Trachylina, are formed instead.

The beautiful analysis of cnidarian development by Berrill (1949, 1950) explains much of what has gone before. The presence or absence of a planula in the life-cycle of scyphozoan and hydrozoan medusae is seen as a function of egg size. Thus the large eggs of the trachymedusan *Liriope* or the scyphozoan *Pelagia* develop directly into medusae. The small eggs of *Gonionemus* and *Cyanea,* on the other hand, develop first into planulae, then into polyps, and finally medusae. The non-ciliated larva of *Haliclystus* is attributable to the minuteness of its egg. The crucial argument is provided by *Aurelia* which has eggs of varying size: the large ones develop directly into medusae; the small ones result in a planula-scyphystoma-medusa type of life-cycle. Intermediate sized eggs sometimes result in elongated swimming forms with a mouth and tentacles at one end: this is clearly an actinula. Thus, the planula and actinula stages would seem to be the result of simple, testable factors rather than the reminiscence of bygone ancestry.

Finally, if this is the case, it might be expected that planulae could be obtainable by experimental techniques. They can. Gilchrist (1937), for example, separated the endoderm and ectoderm of the scyphystoma of *Aurelia aurita* and found that the endoderm would round up into ciliated balls which would stay alive and rotating for days before degenerating. Similarly, depression of ephyrae, through starvation, is manifested by the reduction of the organization through a gastrula to a planula which shows a tendency to attach.

Child (1941) describes the regression of *Corymorpha* hydranths to planula-like forms completely enclosed in periderm in the presence of inhibiting agents such as cyanide, lithium, or alcohol. In echinoderms, sufficient treatment with lithium in the early gastrula stage inhibits endoderm and often renders the ectoderm anaxiate. The resulting ciliated ball of cells, "stereogastrulae," may swim about for two weeks (Child, 1941). Freisling and Reisinger (1958) have studied reconstitu-

tion bodies produced by squeezing pulped planarians through cheesecloth. Ciliated stereoblastula-like bodies form which may even gastrulate. Finally, Holtfreter (1939) isolated ectoderm and mesenchyme from amphibian embryos. The ectoderm grew around the mesenchyme and became ciliated, thus forming an artificial planula.

As a rule all Metazoa, as well as colonial Protozoa, develop from eggs. Therefore, they all must inevitably pass through an ontogenetic stage wherein they consist of a polarized ball of cells which is about the same size as the egg. If the outside cells of the ball are ciliated, then this is a planula. Such a form is best looked on as a special result of the principle that the most probable arrangement of a small mass of relatively undifferentiated adhering cells is a sphere. If the cells can produce cilia, only those bordering the outside will do so, providing other unknown environmental conditions are satisfied. Such an "obligate" view of metazoan embryology has often been stated (see Grimstone, 1959).

It follows, by the same argument, that the phylogeny of *any* multicellular organism must have included an adult form which was a small mass of relatively undifferentiated cells. Consequently, while both Platyhelminthes and Cnidaria, as well as Porifera and Ctenophora, must of course have descended from planuloid ancestors, the question which must now be asked is: were they the *same* planuloid ancestor? The problem is fundamentally insoluble if consideration is given only to "gastraea stages" and their descendants.

Cleavage Patterns

The dissimilarity in the early ontogeny of Porifera, Cnidaria, Ctenophora, and Platyhelminthes is striking and indisputable. Furthermore, the position of these phyla as the most primitive Metazoa lends extra importance to this dissimilarity. Before considering the significance of these embryological differences, we have to deal with the problem: how much of metazoan early ontogeny is metazoan in origin?

In dealing with this question we have first to establish a line of distinction between Protozoa and Proto*metazoa* and then describe, in general, the embryology of any protometazoan. Probably, a good critical difference between colonial Protozoa and simple many-celled animals, *sensu stricto,* is the extent of cellular specialization, that is, the number of different kinds of cells in the organism. Now, some cnidosporidian spores have three types of cells; *Volvox* and *Proterospongia* have only two. On the other hand, a simple sponge (i.e., *Sycon*) is equipped with at least six sorts of cells. The earliest Metazoa must therefore have been, in general, masses of cells of three to five varieties. It is of no consequence what cells they were or where in the organism they were located. Further, devotees of the cellularization theory (Hanson, 1958) would want to postulate a degree of syncytial structure—which is also immaterial to the present argument.

The early embryology of a protometazoan is readily described: it starts as an egg; cleaves to a blastula. If the blastula is solid, only differentiation of the three or four definitive cell-types is needed to complete development. If a blastocoel is present, gastrulation (by invagination or ingression, depending upon size and polarity) follows together with cellular development. If the blastula is a complete or partial syncytium then further development consists of regionation of the cytoplasm by cell membranes.

How much of this embryology must have been inherited from Protozoa? First, sex is widespread among Protozoa. Second, zygotes frequently cleave to produce hollow (*Volvox*) or solid (*Synura*) colonies which correspond morphologically to blastulae. Multiple fission (to satisfy the possibility of cellular origin of Metazoa) also occurs. Third, while gastrulation is largely a metazoan process, the *sorts* of mechanisms employed in gastrulation are already found in Protozoa: involution of

the daughter colonies in *Volvox* (invagination), as well as insinking of reproductive cells in this organism and inwandering of ameboid cells in choanoflagellate colonies (ingression), are examples.

It is clear that the mechanisms of early embryogeny of any given protometazoan were derived from, and were almost identical with, those of its immediate protozoan ancestor. As a corollary if two "Protometazoa" had different cleavages they would probably have had a different protozoan ancestry.

The significance of the temporal position of the lower Metazoa—adjacent to the Protozoa—now becomes clear: the "Protometazoa" described above are obviously "planuloid" ancestors. If the planuloid ancestors inherited their embryology from *their* protozoan forebears, and if the early stages of embryology of the four phyla today are a reflection of the embryology of the planuloid ancestors, then the four phyla are derivable from separate protozoan groups altogether. The key question is: *how stable are the ontological characteristics which differ among the lower phyla;* that is, even if the early embryogenies of these groups are significantly dissimilar today, what are the chances that they were dissimilar in the order of a billion years ago?

Temporal irreversibility being what it is, this problem can be solved only in theory. Evolutionary advances are made by the modification of the late stages of development, when relatively minor portions of the animal are being formed; very early stages are conservative. This conservation results from the fact that mutations in these stages are usually lethal. On this basis it might be expected that egg organization and basic characteristics of the first few cleavages would be relatively unmodified throughout the course of evolution (see Waddington, 1956; Carter, 1954).

The early development of the Cnidaria and Platyhelminthes will now be considered. We need to deduce the probability that the embryologies, as they now exist, have remained substantially unaltered during the metazoan history of the animals. It is also important to find out whether, at points of difference, one embryology might have been derived, as a result of evolutionary modification, from the other. An immediate difficulty is that embryology is notoriously labile in the face of purely physical modifiers such as environment and amount and distribution of yolk. In general, therefore, only isolecithal marine eggs of free-living species should be considered. Other things being equal the early embryology of any two different groups may differ in at least the following characteristics: 1) cleavage pattern, 2) extent of organization of the cytoplasm, and 3) polarity and symmetry.

1) Two lines of evidence indicate that cleavage patterns, *per se,* cannot be considered to be immutable characters:

First of all, it is recognized universally that cleavage pattern is simply another reflection of the underlying developmental organization of the egg. That development can take place without cleavage was already shown by Lillie (1902) who treated *Chaetopterus* eggs with high concentrations of KCl and obtained ciliated bodies which resembled trochophores. Tyler (1941) was also able to produce swimmers without cleavage in *Urechis.*

Secondly, there is no intraphylum uniformity of cleavage, which fact indicates that considerable variation *has* actually occurred in the course of evolutionary history. Even the development of entolecithal turbellarian eggs, while far more uniform than is rare among Cnidaria, still varies considerably from order to order. Early acoelan cleavage is biradial.[1] Ento-

[1] It is often stated that acoelan cleavage is a modification of the spiral type (Dawydoff, 1928; Hyman, 1951; Hand, 1959). Actually, only the second and third cleavage *appear* to be spirally oriented in these forms. It is agreed by all (Gardiner, 1895; Pereyaslawzewa, in Korschelt and Heider, 1895; Georgévitch, 1899; Bresslau, 1909) that the first duet of micromeres circle ninety degrees (or slightly less: Bresslau, 1909) around the "animal-vegetal" axis to lie, finally, athwart

lecithal rhabdocoelan cleavage is spiral but duets, rather than quartettes, of micromeres are given off. Therefore, it is only in the non-primitive Polycladida that one finds the classical spiral pattern seen again in annelids and molluscs.

While a comparison of cleavage pattern from species to species reveals a great deal of variation, a general view of early embryology in cnidarians and flatworms reveals a profound and probably significant difference between them. The variation in developmental pattern among even closely related cnidarians is immense (e.g., Gemmill, 1920). As Berrill (1949) states: "When all the records are taken together . . . . we find a type of organism of almost unbelievable protean plasticity." On the other hand, although cleavage patterns vary from order to order within the Turbellaria, there is intraorder uniformity. The variation in cnidarian embryology is often held up as proof of the primitiveness and ancestral nature of this group. However, the extreme primitiveness of the Acoela coupled with the uniformity of the embryology of these worms betrays this view. Variation of cleavage pattern must be seen as a genuine characteristic of cnidarian embryogeny. That there is no evolutionary connection between these two sorts of developmental pattern is also suggested by the fact that, in spite of the plasticity of cnidarian cleavage, none has ever been found which resembles that of the Acoela or Polycladida.

2) The extent to which the egg cytoplasm is organized and the earliness of the stage at which the developmental pattern is determined are more fundamental and might be more constant distinguishing characteristics than cleavage pattern. However, relatively little experimental work in this direction has been done either with cnidarian or turbellarian material. Zoja (1895a, b), working with medusae, found that late into cleavage the blastomeres remain totipotent. Even $\frac{1}{16}$ blastomeres of *Clytia flavidula* and *Laodice cruciata* would develop into small but normal planulae. On the other hand, $\frac{1}{8}$ blastomeres of other forms (*Geryonia*) cleave to masses of cells which eventually disintegrate (Maas, 1906, 1908; Zoja, 1895b). Gemmill (1920) found that $\frac{1}{8}$ blastomeres of the anemone, *Adamsia*, would develop into a larva with mouth and gastric cavity.

Spiral cleavage, common among Polycladida, is usually associated with a relatively highly organized egg. On the other hand, it is well known that there is no such thing as a fully determinate egg and that some spirally cleaving eggs (*Cerebratulus*) can hardly be considered to be determinate at all. In the absence of experimental evidence on polyclads in particular no conclusions can be drawn regarding the determinacy of spiral cleavage in this order. There has also been no experimental work on acoelan cleavage. In *Microstomum*, a rhabdocoel, early organization of the cytoplasm

---

the apposed cell membranes of the two macromeres. The next cleavage of these two daughter cells is also spirally oriented so that, using the usual notation, the $1a^1$-$1b^1$ axis is at right angles to the $1a^2$-$1b^2$ axis. From this point on, however, all cleavages are strictly biradially arranged. The question is whether this spiral arrangement is due to orientation of the spindle, as in the classical cases, or whether there is a simpler, physical explanation. Aside from the fact that there is no evidence of non-planar spindle position the following points urge the second explanation: 1) In *Polychoerus caudatus* pigment granules outline the future cell boundaries *before* division of the daughter cells begins (Gardiner, 1895). These pigment outlines show the 1d cells in the plane of the macromeres. This suggests that possibly pressure at the plane of abutment increases as cytoplasmic cleavage occurs, causing the duet to slip past each other like a pair of soap bubbles. 2) In the same animal the 2nd cells are also produced in the plane of the macromeres. During cleavage they move toward each other, in fact push the 1d products to either side, and end up abutting each other (Gardiner, 1895). 3) Finally, most of the cleavages in the early embryo are simply not spiral. It would be interesting if such a mechanism were the origin of the classical spiral cleavage of the polyclads. Clearly further investigation of cleavage in Acoela is desirable.

has been demonstrated (Seilern-Aspang, 1957). Two basophilic regions in the egg are noted at the second cleavage. These will become the genital and apical areas of the worm. The fact that this precursor material is not localized in the same blastomere in every egg, while suggesting dissociation between cleavage and determination, might also be traceable to the large amount of yolk in the egg.

There is certainly not enough experimental evidence for assuming that platyhelminth eggs and early embryos are more highly organized than those of Cnidaria. On the other hand the contrasting nature of the cleavage patterns and the ability of isolated late cnidarian blastomeres to reconstitute a complete developing system, suggest that this is the case.

3) The symmetry of the cleaving egg in the primitive members of the two phyla is an unvarying feature differentiating between Cnidaria and Platyhelminthes. The early embryos of *all* the primitive Acoela are biradially symmetrical beginning with the second cleavage.[2] Bilateral symmetry appears later, after gastrulation. On the other hand, the hydrozoans are all radially symmetrical from the egg on. It is only in the Anthozoa that bilaterality finally appears but not in early cleavage.

Hand (1959) notes that, on the basis of their drastically different symmetry and polarity, the platyhelminth and cnidarian lines must have diverged very early from the common planuloid ancestral type. That this is true is not to be doubted. However, the assumption stated earlier, that the symmetry and cleavage pattern of the animals are approximately the same as their separate planuloid ancestors, if accepted, leads to the conclusion that the divergence occurred at the protozoan level of organization. On this view the Cnidaria have sprung from Protozoa with haphazard, and therefore radial, probably indeterminate, cleavage. The Platyhelminthes are derived from other Protozoa with orderly, biradial (or bilateral), probably determinate, egg cleavage.

[2] See footnote 1.

Symmetry

The assumption that the Eumetazoa had a common multicelled ancestor leads necessarily to another: that there must likewise have been some primitive kind of symmetry. Of the latter there are three possibilities: 1) radial (Cnidaria), 2) bilateral (Platyhelminthes), or 3) biradial (Ctenophora).

The approach to the origin of all Metazoa from a bilateral ancestor is taken by Hadži (1953), Hanson (1958), and Jägersten (1955). This view encounters difficulty when it attempts to describe the origin of the Cnidaria, a group which is basically radially symmetrical. The resulting absurdities have been explored by Hyman (1959) and Hand (1959).

The origin of the "Bilateria" from a radially symmetrical, presumably cnidarian ancestor is more easily defended (see Hyman, 1952) and believed. However, bilateral symmetry has emerged separately in all the groups of Protozoa and even within the Cnidaria. In fact, this is such a common occurrence in the animal kingdom that, while conceding that the Platyhelminthes must have had a radial ancestry, it seems unwarranted for the assumption to be made that this ancestry must also have been that of the Cnidaria.

The symmetry difficulty disappears if the Metazoa arose polyphyletically. There are, in fact, two sorts of arguments which suggest that flatworms probably did not arise from the cnidarian stock:

1) As has already been stated, the embryonic symmetries of the two groups are exclusively distributed. This is generally true for adult forms as well as developmental stages. That this distribution is independent of the supposed primitiveness of the groups has already been mentioned in the discussion of embryology.

The mutual exclusiveness of symmetry is also unrelated to the supposed primitive ecology and habit of the animals.

Cnidarian polyps have been associated with the evolutionary stimulus of the substrate for at least as long as have the flatworms. Furthermore, a good number of the polyps are *not* sessile. Yet there are no flattened, creeping cnidarians as a result of this long selective stimulus. The simple fact is that the oral-aboral polarity is very strong; these animals have never "learned" to differentiate and grow in any direction other than along this axis. In the Cnidaria it is this characteristic of growth which *leads* to sessility and not *vice versa.* When differentiation and growth at right angles to this axis finally appears in the Anthozoa, it is but weakly impressed. In the regeneration of anthozoans, in particular *Metridium,* bilateral symmetry is easily lost . . . . the animal does not care enough to count its own septa.

Similarly, the flatworms, whether pelagic or substrate bound, have never lost their bilaterality. Thus the planktonic acoelan, *Haplodiscus piper,* remains bilaterally symmetrical. Even the pelagic Müller's larva is bilateral.

Hand (1959) and others have noted that the sessile and pelagic habits lead to radial symmetry. This is, of course, true. However, it is also true that radial symmetry is, *in fact, never* achieved. The basic symmetry of the animal remains apparent to the observer.

2) Where it is highly probable that bilateral animals *have* been derived from radial ones (gymnostomes to hymenostomes, Hydrozoa to Anthozoa) there is no doubt of the fact that *at least* the animals involved are otherwise closely related. Such evidence, which might support the supposed Cnidaria-Platyhelminthes transformation, is lacking. The morphology and physiology of the flatworms and cnidarians are profoundly different. The dissimilarities have been admirably described by Hyman (1959) and Hand (1959) as arguments against the derivation of Anthozoa from rhabdocoels. These arguments are, however, also effective in suggesting that the flatworms could not, by the same token, be derived from cnidarian stock. The deep-rooted differences in symmetry, unalterable by long environmental pressure, would seem to emphasize the improbability of common ancestry.

Conclusions

It has been suggested here that a common planuloid ancestor for Eumetazoa cannot be assumed to exist on the basis of a planula or stereogastrula stage in metazoan embryology. It was demonstrated that all Protometazoa had to be planuloid whether or not they were related. On the basis of radically different early embryology—in particular with regard to strictness of pattern and symmetry of the cleaving egg—and on the assumption that these characteristics of the embryology are stable with time, it was suggested that, so far as their history *as Metazoa* is concerned, the cnidarians are primitively radially symmetrical and the Platyhelminthes are primitively bilaterally symmetrical. Thus, the origin of the Cnidaria and Platyhelminthes is to be found in separate groups of Protozoa. It was shown how such a move would solve the symmetry problem.

There are a few loose ends which need to be tied. The problem of the Ctenophora has been studiously avoided. These animals resemble the Cnidaria in their general body construction and in the presence of the unbending animal-vegetal axis. However, while the biradial symmetry of ctenophores obviously *might* have been derived from the tetramerous radial symmetry of hydrozoan medusae such a derivation is not at all *necessary.* The strict determinate biradial cleavage of ctenophores is well-known and resembles (at least more than anything else) the early cleavage of Acoela. The possibility that their mesoderm is endodermal in origin (Metschnikoff in Hyman, 1940) is also flatworm-like. Another feature which the Ctenophora hold in common with the flatworms is their ability to react to the stimulus of the substrate by flattening out on it blastopore down. Of course,

the result is quite different, and this particular characteristic (flattening) is one which has arisen many times (*Euplotes*) and in non-homologisable. The presence of endogenous nematocysts in a single species of Ctenophora, as much as illuminating the phylogeny of Ctenophora, would seem to obscure the significance of nematocysts as valid phylogenetic markers. As far as the Ctenophora are concerned, the safest and most consistent course, from the standpoint of this paper, would be to assume that they also arose from a separate group of Protozoa.

If the primitive Metazoa have, in fact, been derived polyphyletically, further consideration should probably be given to their possible protozoan ancestry. The Cnidaria and Porifera have probably arisen from radially symmetrical colonial Protozoa. The arguments which urge the origin of the sponges in some choanoflagellated protomonad colony are well known. The recent refinding of *Proterospongia* by Lackey (1959) increases the possibility that a suitable ancestral colony of this type did exist.

In suggesting, as an opposing hypothesis, that Cnidaria could have come from coenobial volvocine colonies, Hanson (1958) set up a straw man to knock down. The regular, determinate cleavage of these colonies of course excludes them from Cnidarian ancestry. Clearly, a non-coenobial flagellated colony with haphazard cleavage is what is needed. Perhaps *Synura* is a good *model.*

For the derivation of the flatworms there are two possibilities. One is the theory originally stated by Hadzi (1953) which derives them by cellularization of a ciliate. There is no need to elaborate on the exposition of this view by Hanson (1958) although his ecological arguments are doubtless of little phylogenetic value.

Another theory is one which Hanson discards. The flatworms (and Ctenophora) with their regular cleavage might very well have had coenobial (but not volvocine) colonies as their ancestors. Such a view was suggested by Van Cleave (1932). The eutelic, bilateral dicyemid mesozoans serve as an excellent, and obvious, model of what a pre-planuloid platyhelminth might have looked like.

There have been many attempts at multicellularity among organisms. The fungi, various groups of algae, higher plants, and sponges are agreed by all to have come from different groups of unicellular organisms. Even the many colonial protozoa and the multinucleate forms can be viewed as attempts at multicellularity. It is odd that attempts should be made at all to derive such different organisms as Cnidaria, Ctenophora and Platyhelminthes from a common metazoan ancestor.

REFERENCES

BADER, R. S. 1958. Similarity and recency of common ancestry. Syst. Zool., 7:184–187.

BERRILL, N. J. 1949. Developmental analysis of scyphomedusae. Biol. Rev., 24:393–410.

——— 1950. Development and medusa-bud formation in the Hydromedusae. Quart. Rev. Biol., 25:292–316.

BRESSLAU, E. 1909. Die Entwicklung der Acoelen. Verhandl. Deutsch. Zool. Gesell., 19:314–324.

CARTER, G. S. 1954. On Hadži's interpretations of animal phylogeny. Syst. Zool., 3:163–167.

CHILD, C. M. 1941. Patterns and problems of development. University of Chicago Press, Chicago.

DAWYDOFF, C. 1928. Traité d'embryologie comparée des invertébrés. Masson et Cie, Paris.

FREISLING, M., and REISINGER, E. 1958. Zur Genese und Physiologie von Restitutionskörpern aus Planariengewebsbrei. Arch. Entw'mech., 150:581–606.

GARDINER, E. G. 1895. Early development of *Polychoerus caudatus* Mark. Jour. Morphol. 11:156–176.

GEMMILL, J. F. 1920. The development of the sea-anemones *Metridium dianthus* (Ellis) and *Adamsia palliata* (Bohad). Philos. Trans. Roy. Soc. London, Ser. B., 209:351–375.

GEORGÉVITCH, J. 1899. Étude sur le développement de la *Convoluta roscoffensis* Graff. Arch. Zool. Exptl. Gén., 7:343–361.

GILCHRIST, F. G. 1937. Budding and locomotion in the scyphistomas of *Aurelia.* Biol. Bull., 72:99–124.

GRIMSTONE, A. V. 1959. Cytology, homology and phylogeny—a note on "organic design." Amer. Natural., 93:273–282.

HADŽI, J. 1953. An attempt to reconstruct the system of animal classification. Syst. Zool., 2:145–154.

HAND, C. 1959. On the origin and phylogeny of the coelenterates. Syst. Zool., 8:191–202.

HANSON, E. D. 1958. On the origin of the Eumetazoa. Syst. Zool., 7:16–47.

HOLTFRETER, J. 1939. Gewebeaffinität, ein Mittel der embryonalen Formbildung. Arch. Exptl. Zellforsch., 23:169–209.

HYMAN, L. H. 1940. The Invertebrates, Vol. I. Protozoa through Ctenophora. McGraw-Hill Book Co., New York.

——— 1951. The Invertebrates, Vol. II. Platyhelminthes and Rhynchocoela. McGraw-Hill Book Co., New York.

——— 1959. The Invertebrates, Vol. V. Smaller coelomate groups. McGraw-Hill Book Co., New York.

JÄGERSTEN, G. 1955. On the early phylogeny of the Metazoa. Zool. Bidrag, 30:321–354.

KORSCHELT, E., and HEIDER, K. 1895. Textbook of the embryology of invertebrates. Part I. Porifera, Cnidaria, Ctenophora, Vermes, Enteropneusta, Echinodermata. Macmillan Co., New York.

LACKEY, J. B. 1959. Morphology and biology of a species of *Protospongia*. Trans. Amer. Micros. Soc., 78:202–206.

LILLIE, F. R. 1902. Differentiation without cleavage in the egg of the annelid *Chaetopterus pergamentaceus*. Arch. Entw'mech., 14:477–499.

MAAS, O. 1905. Experimentelle Beiträge zur Entwicklungsgeschichte der Medusen. Ztschr. Wiss. Zool., 82:601–610.

——— 1908. Über den Bau des Meduseneis. Verhandl. Deutsch. Zool. Gesell., 18:114–129.

PICKEN, L. E. R. 1953. A note on the nematocysts of *Corynactis viridis*. Quart. Jour. Microsc. Sci., 94:203–227.

——— 1957. Stinging capsules and designing nature. New Biology, no. 22:56–72.

SEILERN-ASPANG, F. 1957. Die Entwicklung von *Macrostomum appendiculatum* (Fabricius). Zool. Jahrb., Abt. Anat. Ontog. Tiere, 76:311–330.

SLAUTTERBACK, D. B., and FAWCETT, D. W. 1959. The development of the cnidoblasts of *Hydra*. An electron microscopic study of cell differentiation. Jour. Biophys. Biochem. Cytol., 5:441–452.

TYLER, A. 1941. Artificial parthenogenesis. Biol. Rev., 16:291–336.

VAN CLEAVE, H. J. 1932. Eutely or cell constancy in its relation to body size. Quart. Rev. Biol., 7:59–67.

WADDINGTON, C. H. 1956. Principles of embryology. George Allen and Unwin, London.

WEILL, R. 1946. *Ctenoctophrys chattoni* n. g., n. sp., infusoire planctonique octoradié, à caractére de méduse et de ctenophore. C. R. Acad. Sci. Paris, 222:683–685.

ZOJA, R. 1895a. Sullo sviluppo dei blastomeri isolati dalle uova di alcune meduse (e di altri organismi). Arch. Entw'mech., 1:578–595.

——— 1895b. Sullo sviluppo dei blastomeri isolati dalle uova di alcune meduse (e di altri organismi). Arch. Entw'mech., 2:1–37.

MICHAEL JOHN GREENBERG is instructor in zoology at the University of Illinois in Urbana.

Index for Volume 8 (1959)

BIGELOW, R. S. Similarity, ancestry, and scientific principles 165

BLACKWELDER, R. E. The present status of systematic zoology 69

BLACKWELDER, R. E. The functions and limitations of classification 202

BUCHANAN, R. E. The international code of nomenclature of the bacteria and viruses 27

CORLISS, J. O. Comments on the phylogeny and systematics of the Protozoa 169

GOSLINE, W. A. Mode of life, functional morphology, and the classification of modern teleostean fishes 160

GREENBERG, M. J. Ancestors, embryos, and symmetry 212

HAND, C. On the origin and phylogeny of the coelenterates 191

HYMAN, L. H. Further remarks on the word nema 57

IRWIN, M. R. Interrelationships of genetic characters which differentiate species of doves (*Streptopelia*) 48

IVANOV, A. V. The nervous system of Pogonophora 96

JOHNSON, M. L., and WICKS, M. J. Serum protein electrophoresis in mammals—taxonomic implications 88

KECK, D. D. The future of systematic botany 76

KELLOGG, R. Introduction to symposium 59

KIRIAKOFF, S. G. Phylogenetic systematics versus typology 117

KREKELER, C. H. Dispersal of cavernicolous beetles 119

LEVI, H. W. Problems in the spider genus *Steatoda* (Theridiidae) 107

LINSLEY, E. G., and USINGER, R. L. Linnaeus and the development of the International Code of Zoological Nomenclature 39

PIMENTEL, R. A. Mendelian infraspecific divergence levels and their analysis 139

RICKETT, H. W. The status of botanical nomenclature 22

ROLLINS, R. C. Linnaeus: Codes and nomenclature in biology 2

STAFLEU, F. A. The present status of plant taxonomy 59

STEARN, W. T. The background of Linnaeus's contributions to the nomenclature and methods of systematic biology 4

WHARTON, G. W. Introduction to Linnaean bicentennial 1

WHARTON, G. W. The future of systematic zoology 82

WHITTEN, J. M. The tracheal system as a systematic character in larval Diptera .. 130

SYSTEMATIC ZOOLOGY is published quarterly by the Society of Systematic Zoology. Its purpose is threefold: To publish, and therefore to encourage the preparation of, contributions on basic aspects of all fields of systematics, principles and problems; to provide a suitable forum for discussion of the problems of the systematist and his methods; and to report as news the other activities of the Society of Systematic Zoology.

Contributions of the following types are solicited: Papers on principles and the applications of principles of wide implication and general interest in any phase of systematics, such as comparative anatomy, zoogeography, paleontology, taxonomy, classification, evolution, or genetics; discussions of methods, specific problems, and activities of systematists; discussions of new books and monographs; and news of systematists, organizations interested in systematics, research and teaching programs, expeditions, collections, meetings, and anything else of interest to systematists.

Manuscripts must be mailed flat, not folded or rolled. They must be typed double-spaced on standard typewriter paper, with ample margins on all four sides. Double-spacing applies to all parts of the manuscript—footnotes, legends of figures, literature list, tables, etc. Footnotes are numbered consecutively and may be placed in the text between horizontal lines or listed on a separate page. Literature list will be headed REFERENCES and will follow style in recent issues of the journal, thus: name of author, year, exact title, journal name abbreviated, volume number, first and last pages. Journal abbreviations may follow usage in *Biological Abstracts*. Avoid excessive abbreviation as in the *World List*, not recommended. Journal names consisting of a single word (*Science, Evolution, Genetics,* etc.) are written out in full, as are also names of unusual or rare journals. Geographic names (*London, California*) are not abbreviated. Number of issue of a journal is not wanted unless such issues are repaged. Number of figures and plates may be omitted. Books are referred to as follows: author, year, exact title, name of publisher, location of publisher. Tables are typed on separate sheets placed in correct sequence in the text. Tables are expensive to set and should be limited to the strictly necessary. Avoid vertical lines. Illustrations should preferably be prepared for reproduction as line cuts, but illustrations requiring half-tone reproduction are acceptable. Illustrations are usually made larger than, but not more than twice as large as, their eventual size in the published journal. In preparing illustrations, the dimensions of the printed page (8 x 5¼ inches) should be kept in mind. Figure legends are typed on a separate page placed at the end of the manuscript. The full scientific name of an animal, including the author and year, must be given the first time the animal is mentioned.

Authors receive galley proof accompanied by a reprint order and are reminded that changes in proof are expensive. They should not attempt to rewrite the article on the galley proof. The cost of alterations made in proof will be charged to the author if it exceeds ten per cent of the cost of composition. Authors should inform the editor whether or not they wish the original illustrations returned. To avoid delay authors with articles in press should keep the editor informed of any permanent or temporary change in address.